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PORCELLIDIIDAE OF AUSTRALIA (HARPACTICOIDA, COPEPODA)

I. A REASSESSMENT OF THE EUROPEAN SPECIES OF *PORCELLIDIUM*

II. THE IMPORTANCE OF THE MALE ANTENNULE IN TAXONOMY

III. SYNOPSIS OF GENERA AND SPECIES

by

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Porcellidiidae of Australia (Harpacticoida, Copepoda). I. A Reassessment of the European Species of *Porcellidium*

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Abstract. A new species, *Porcellidium rastellum*, is described from NSW bringing the total number of species in that genus for Australia to seven. Unlike other Australian genera in the Porcellidiidae, *Porcellidium* Claus, 1860 is ill defined. *Porcellidium viride* (Philippi, 1840) is considered the type species to the genus, but it has never been adequately characterized. This has led to considerable disagreement on the characters that define the genus. *Porcellidium viride* can be identified from a species specific character shown by Brady's (1880) drawing of the male antennules. Another species, *Porcellidium fimbriatum* Claus, 1863, can also be identified by species specific characters shown in the more complete description by Claus (1889). This enables new specimens of these two species to be identified with a high degree of certainty. In the present study, specimens collected from Oban, Scotland, identified as *P. viride* and *P. fimbriatum*, have been used to redescribe both species in detail and select species specific characters for a diagnosis of each species. A new diagnosis for the genus *Porcellidium* is given, based on the characters of *P. viride*. Extensive enquiry suggests that Philippi's and Claus' type material is lost. To ensure taxonomic stability of the genus *Porcellidium,* a neotype of *P. viride* is designated. From this study it is shown that *P. lecanoides* Claus, 1889 and *P. sarsi* Bocquet, 1948 are junior synonyms for *P. viride*. The new diagnosis for *Porcellidium* excludes many of the species originally placed in that genus. *Porcellidium tenuicauda* Claus, 1860 and *P. scutatum* Claus, 1889 are examples of species that possess apomorphic characters excluding them from *Porcellidium* sensu stricto. A new genus, *Porcelloides* gen. nov. is proposed to take Claus' two species, as *Porcelloides tenuicaudus* (Claus, 1860) comb. nov., and *Porcelloides scutatus* (Claus, 1889) comb. nov. Keys to the known species of *Porcellidium* and *Porcelloides* are given.

Keywords: Porcellidiidae, *Porcellidium*, *Porcelloides.*

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Considerable progress has been made in our understanding of the family Porcellidiidae from recent studies on the fauna of the West Pacific Ocean. The works of Gamô (1969), Ho (1986), S. Kim & W. Kim (1996), Harris & Iwasaki (1996a,b), Il-H. Kim & H.-S. Kim, (1997) and Harris & Iwasaki (1997, 2009) have described in detail 17 new species from Japan and Korea while another 23 new species have been described from Aotearoa (New Zealand) and Australia,

Hicks (1971), Hicks & Webber (1983), Harris & Robertson (1994), Harris (1994, 2002), Walker-Smith (2001). These studies provided a wealth of information on porcellidiid structure and a clearer understanding of the wide range of features that could be used as taxonomic characters.

Many of the new species collected from Australia could not be assigned to *Porcellidium* as understood at that time. This led Harris & Robertson (1994) and Harris (1994) to erect five new genera to accommodate the rejected species. Huys *et al*. (1996) considered that these new genera were "based on dubious grounds" and "without any prior revision of the highly speciose type genus *Porcellidium* it does not seem justified to maintain these Australian genera." The problem was that *Porcellidium viride* Philippi, 1840 had never been described in sufficient detail to compare it with the Australian species, despite the fact that it is considered the type species to the genus. Without a detailed description of both male and female of the type species it was impossible to give a definitive diagnosis for *Porcellidium*.

Among recent authors there is no complete agreement on the characters that define *Porcellidium*. The diagnoses of Harris & Robertson (1994), Huys *et al.* (1996), Harris & Iwasaki (1996) and Walker-Smith (2001) all fail on the following grounds: *(a)* there is no clear statement as to the criteria upon which genera are defined, *(b)* absence of detailed information about males of the four European species upon which the genus is based and *(c)* freedom from the ideas and synonymies of previous authors, such as Lang (1948). The description of Japanese and Australian species have provided a wealth of information on fine morphological detail, particularly of the male antennule, and a clearer understanding of the range of apomorphic and plesiomorphic characters that can be used for taxonomic purposes. Walker-Smith (2001) has pointed out that genera should be based on apomorphic characters and it can be shown that the new genera proposed by Harris & Robertson (1994), Harris (1994, 2002), Harris & Iwasaki (1996b, 1997, 2009) all display apomorphies that separate them from one another.

Porcellidium is no longer regarded as the only genus in the Porcellidiidae. *Tectacingulum* and *Brevifrons,* Harris (1994) and *Clavigofera* and *Kushia*, Harris & Iwasaki (1996b) have been accepted by Bodin (1997), Walker-Smith (2001) and Wells (2007). *Dilatatiocauda* Harris (2002) has been accepted by Wells (2007). But the genus *Porcellidium* still remains poorly defined and the number of species that should be assigned to it is uncertain. It is important, therefore, that the European species, upon which *Porcellidium* was originally based, should be redescribed in detail so that a new diagnosis can be given for the genus.

A description of *Porcellidium viride* was given by Brady (1880). Although this description is inaccurate and hopelessly confused, his illustration does show one species specific character (related to the male's antennule) that makes it possible to recognize the species with a high degree of certainty. Consequently it has been possible to identify specimens, collected from Scotland in the present study, as *Porcellidium viride*. This enabled a full redescription of the species to be made with a clearer understanding of its species specific characters. *Porcellidium viride* is regarded as the type species to the genus (Apostanov & Marinov, 1988) and so it is now possible to give a definitive diagnosis for the genus *Porcellidium* from the new description of *P. viride*. To give taxonomic stability to the taxon, an adult male *P. viride* collected at Clachan, Seil Sound, Oban is designated as the neotype. Among other places in Scotland, Brady records the species from Loch Fyne not far from Seil Sound, Oban. Brady (1880) misidentified the adult female of his *P. viride* and called it *Porcellidium fimbriatum*. This was largely due to the inadequate description Claus (1863) gave for *P. fimbriatum*, but the error was perpetuated by other early authors, Thompson & Scott (1903), Sars (1904), Monard (1928), Lang (1948), (see also Appendix 1).

In 1889 Claus redescribed *Porcellidium fimbriatum* and his illustrations show species-specific characters that allowed positive identification of animals collected from Oban, Scotland. The species is redescribed in detail.

A direct consequence of re-diagnosis for *Porcellidium* is that many species originally placed in that genus are now excluded and must be assigned to other genera. For example *Porcellidium tenuicauda* Claus, 1860 and *P. scutatum* Claus, 1889 both have apomorphic characters that are not found in *Porcellidium* or any other genera of the Porcellidiidae. It is proposed to assign them to a new genus, *Porcelloides* gen. nov., as *Porcelloides tenuicaudus* (Claus, 1860) comb. nov., and *Porcelloides scutatus* (Claus, 1889) comb. nov.

The new descriptions of European species means that they can now be compared with Japanese and Australian species to expand our understanding of character diversity in the family.

Methods and nomenclature

Longitude and latitude of collecting sites were made by extrapolation from Ordinance Survey maps and are only approximate. Dates are given as day/month/year.

Animals were collected by washing a sample of seaweed for about three minutes in a bucket containing a 50/50 mixture of soda water saturated with CO_2 (from soda siphon or bottled soda water) and fresh water. This appears to anaesthetize copepods and other small marine animals, these were then collected by removing the seaweed, allowing another three minutes for the animals to sink to the bottom and then pouring off most of the water (which was used again). Five percent formalin was then added to fix the animals. Porcellidiid copepods were extracted using a dissecting microscope and then preserved in 5% borate buffered formalin. This method of collection has the advantage that the male antennule remains fully extended and is easy to study. Specimens usually retain their colouration for several years in the buffered formalin.

For each new Australian species an adult male was chosen as holotype and an ovigerous female as allotype from the type series selected from one of the samples washed from seaweeds. Nearly all the illustrations are drawn from paratype material. This is because fine details that show species specific characters are difficult to measure or draw from the type specimens without dissection. To overcome this problem, paratype specimens from the type series were dissected and used to draw the unique and general structures of each species. Dissections were mounted in polyvinyl lactophenol. Drawings were made either by means of a drawing-tube attachment or from digital photographs. Numbers on some of the drawings refer to the slides from which they were drawn. Measurements were made using a calibrated micrometer eyepiece or from calibrated digital

photographs. The delicate hyaline membrane that surrounds the cephalosome and metasome segments is not shown in the drawing of adult animals, but may be illustrated in detail elsewhere. The extremely fine hair-like setules and "feathering" of setae found on mouthparts and ambulatory limbs is only indicated diagrammatically in the drawings.

Terminology follows Harris & Robertson (1994). Members of the Porcellidiidae are poor swimmers. Their antennae and limbs P2, P3 and P4 are highly specialized for movement over the surface of seaweed and will be referred to as "ambulatory limbs". Comparison of caudal setae with other copepods is difficult because the furca is modified for protecting the egg mass. The rami are flattened and the setae greatly shortened. There are two dorsal setae (α and β) plus a third (γ) which is usually inserted at the lateral region of the posterior border. Typically there are four terminal setae (T1–T4) on the posterior border of the caudal ramus (Figs 21E, 22H), but T1, T2 or T3 may be missing on certain species. Wells (2007:871, fig. 120) gives a diagram illustrating the differences between the above notation and that of Huys & Boxshall (1991). The terms "serrulate" is used to denote very fine short serration on setae, "plumulose" is used to describe very fine "feathering" on antennule setae and "pinnate" for fine feathering on terminal caudal setae. Because the caudal rami can be held in line with the body or depressed downwards, some animals may appear much shorter than others. A more reliable measure is the distance from rostrum to the extremity of the genital double-somite. This is denoted by the symbol L_{urs} and the distance to the extremity of the caudal furca by the symbol L_{max}. The male antennule is measured in the fully extended position. The position of α and β seta relative to the posterior border of the female caudal ramus is a useful parameter in distinguishing between some species. Here it is expressed as the Hick's index defined as the distance of either α or β seta from the posterior border of the ramus divided by the length of the ramus expressed as a percentage (i.e., α/ramus length × 100).

The following abbreviations are used. NHM—Natural History Museum, London; NMI—National Museum of Ireland, Dublin; AM—Australian Museum, Sydney.

Systematics

Family Porcellidiidae Boeck, 1865

Type genus: *Porcellidium* Claus, 1860

Diagnosis. Antennule of adult male subchirocer, six segmented, less than half body width, segment 3 partly fused with segment 4, coupling denticles on ventral surface of segment 4; antenna exopod of one segment with six setae; large mandibular palp, anterior lobe with four bulbous setae, posterior lobe with one annulate seta and five bulbous setae, endopod with nine setae; cephalosome surrounded by hyaline membrane (in one genus the hyaline membrane is located on the ventral surface of the cephalosome) with eight embedded border sensilla (six or seven sensilla in species where the anterior border of the cephalosome is turned ventrally); epipleural lobe of metasome segment 3 expanded in male, reduced in female; urosome consists of 5th somite, genital double-somite, anal somite and caudal furca; furca composed of two flat plates or rami each with seven setae, setae never longer than ramus, (α and β dorsal, γ terminal, plus four terminal setae [may be reduced to three or two in some species]); strong sexual dimorphism.

Generic composition. *Porcellidium* Claus, 1860; *Tectacingulum* Harris, 1994; *Murramia* Harris, 1994; *Brevifrons* Harris, 1994; *Acutiramus* Harris & Robertson, 1994; *Clavigofera* Harris & Iwasaki, 1996b; *Kushia* Harris & Iwasaki, 1996b; *Kensakia* Harris & Iwasaki, 1997; *Mucrorostrum* Harris & Iwasaki, 1997; *Dilatatiocauda* Harris, 2002; *Porcelloides* gen. nov.

Genus *Porcellidium* Claus, 1860

Type species. *Porcellidium viride* (Philippi, 1840).

Diagnosis [an alternative (apomorphic) character state is known for all characters marked with an asterisk]. Spermatophore elongate* (sausage shaped), female receives only one spermatophore during her life span, usually deposited on ventral surface of the genital double-somite at time of metamorphosis from stage V copepodid to adult, attachment to female ephemeral (shed before egg laying starts); body oval*, dorsoventrally compressed*; male cephalosome truncated anteriorly*, female not truncated anteriorly*; animals do not conglobate*; dorsal organs absent*, no massive honeycomb-like cuticle; hyaline border surrounds cephalosome*, marginal glands open dorsal to hyaline border*; female genital double-somite broad*, divided into anterior and posterior lobes*, rounded posteriorly*, lateral striations absent*; male genital somite never fused to metasome segment 4 and P5 baseoendopod*; female caudal ramus rectangular*, setae T1 to T4 always present* (T1 may be recessed), never pinnately clavate or evenly spaced*; no ridge-plates on labrum*; six setae on maxillule endopod*; maxilliped coxae touch in midline*, basis with fimbriate process*; limbs P2, P3, P4 with three external spinous setae on exopod segment 3*; P5 shorter than genital double-somite*, ventral expansion absent*; male antennule segment 3 setae δ and δ' always present*, anterior comb absent*, blade or knob-like ventral process may be present, segment 4 with three denticles*, brush-pad never present*; male P5 trapezoid with six setae*.

Species composition. *Porcellidium viride* (Philippi, 1840); *P. fimbriatum* Claus, 1863; *P. roscoffensis* (Bocquet, 1948) comb. nov. (northeast Atlantic coast of Europe and Mediterranean Sea); *P. rubrum* Pallares, 1966 (Argentina); *P. erythrum* Hicks, 1971 (Aotearoa, New Zealand); *P. hartmannorum* Tiemann, 1978; *P. algoense* Hicks, 1982 (East and West coast of South Africa); *P. hormosirii* Harris & Robertson, 1994; *P. ocellum* Harris & Robertson, 1994; *P. pulchrum* Harris & Robertson, 1994; *P. erythrogastrum* Harris & Robertson, 1994; *P. naviculum* Harris & Robertson, 1994; *P. phyllosporum* Harris & Robertson, 1994; *P. londonarum* Harris, 1994 (name correction for *P. londonii* by Wells, 2007); *P. rastellum* sp. nov. (East Coast of Australia); *P. ofunatense* Harris & Iwasaki, 1996; *P. kiiroum* Harris & Iwasaki, 1996; *P. akashimum* Harris & Iwasaki, 1996; *P. wandoensis* Kim & Kim, 1997; *P. brevicavum* Kim & Kim, 1997 (Japan and Korea).

Key to the species of *Porcellidium*

The antennules of male porcellidiids provide numerous species specific characters, consequently any male animal, for which the antennule has been described in detail, can be identified with a high degree of certainty. In marked contrast, very few species specific characters have been found on female members of the genus *Porcellidium*, consequently the females of less than half of the 20 recognized species can be identified. This is because female characters are based upon shape, position, size or number of body parts which will vary within a species and their measurements or ratios may overlap with other species.

The following key will rely heavily on characters of the male antennule which must be viewed from the ventral side in the fully extended position (see *Methods and nomenclature*). Female ratios are given to help confirm the identity of the female animals. [Abbreviations: *CR* caudal ramus; *GDS* genital double-somite; *L* length of animal; *H.I.* Hicks' index for α or β setae; * see Hicks, 1982:64].

1 Male antennule with ventral process or "blade" on segment 3 (see Fig. 12D, F) 2

—— Male antennule with "peg" or swollen knob on segment 3 (see Fig. 7F) 3

—— No blade, peg or knob on segment 3 of male antennule 4

2 Ventral process short (¼ length of segments 3+4), coupling denticle 1 on segment 4 flat with serrated edge, denticles 2 and 3 very small, botryoidal, segment 6 distinct (not fused with segment 5). Ventral surface of male and female cephalosome wrinkled (Fig. 12A). Female GDS with deep cleft between anterior and posterior lobe. Body length male 0.56 mm, female 0.77 mm, CR/L = 18%, CR l/w = 2.8, H.I. for β = 25%, setae T1–T4 pinnate. Colourless with broad band of dark blue down middle of back. Europe. (Plate 1C,E, p. 67) ..... *P. fimbriatum* (Claus, 1863)

—— Ventral blade almost as long as segments 3+4, segment 3 with spine ventral to δ seta, denticle 1 on segment 4 comb-like, 2 and 3 serrate, segment 5 hooked, fused with 6. Body length male 0.55 mm, female 0.71 mm, CR/L = 7%, CR l/w = 1.2, H.I. for β = 20%. Colour yellow with broad red dorsal stripe. Australia. (Plate 2B, p. 69) ..... *P. pulchrum* Harris & Robertson, 1994

—— Ventral blade bifid, ½ length of segments 3+4, denticle 2 on segment 4 spherical with surface serrations, denticle 3 large flat triangle with distal border serrated, segment 5 not hooked fused with 6. α seta on female CR thicker than other setae. Body length male 0.50 mm, female 0.68 mm, CR/L = 12%, CR l/w 1.7, H.I. for β = 22%. Amber colour. Australia ..... *P. hormosirii* Harris & Robertson, 1994

—— Ventral blade ½ length of segments 3+4, segment 3 with finger-like lobe pointing forward ventral to δ seta, denticles 1, 2 and 3 triangular with double serrated edge, segment 6 fused with 5. Body length male 0.56 mm, female 0.67 mm, CR/L = 6%, CR l/w 1.5, H.I. for β = 32%, GDS with lateral notch. Colourless with red area round ocellus and larger red dot in middle of back. Australia. (Plate 2H, p. 69) ..... *P. ocellum* Harris & Robertson, 1994

—— Ventral blade ½ length of segments 3+4, denticle 1 on segment 4 comb-like, 2 and 3 with serrated edge, segment 5 small, fused with 6. Body length male 0.61 mm, female 0.83 mm, CR/L = 5.5%, CR l/w 1.45, H.I. for β = 10%, GDS with lateral notch. Colourless with areas of thickened ventral cuticle dark red. Australia. (Plate 2A, p. 69) ..... *P. erythrogastrum* Harris & Robertson, 1994

—— Ventral blade ¾ length of segments 3+4, denticle 1 on segment 4 double serrated, 2 tooth-like, 3 with serrated edge, segment 5 hooked, fused with 6. Body length male 0.57 mm, female 0.75 mm, CR/L = 11%, CR l/w 2.2, H.I. for β = 9%, GDS with scar and very small notch. Coral pink with small iridescent light blue areas at trabeculae, GDS scar and between metasome segments. Australia. (Plate 2F, p. 69) ..... *P. londonarum* Harris, 1994

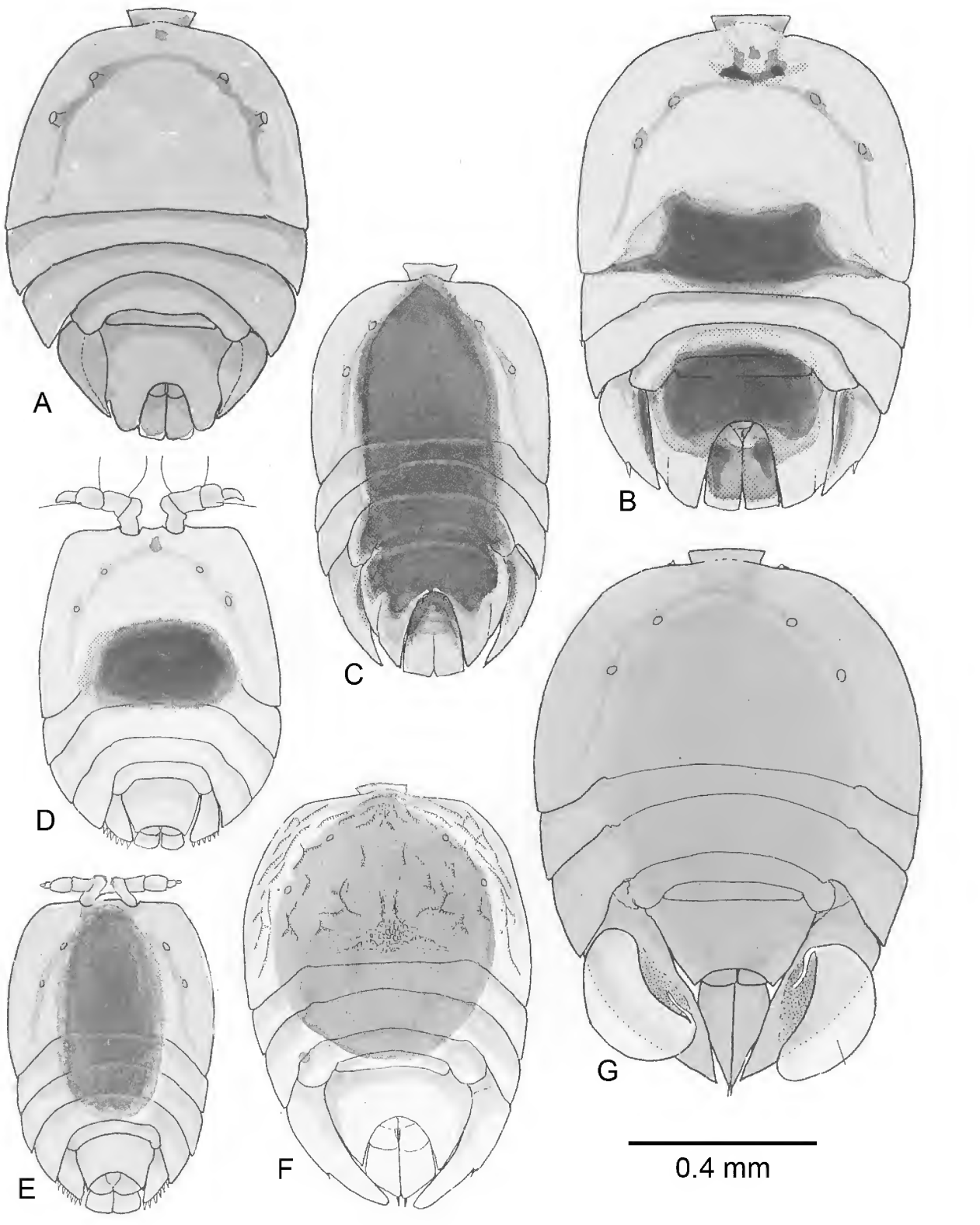

Plate 1. *(A) Porcellidium rastellum* sp. nov., female (Australia). *(B) Porcellidium viride* Philippi, 1880, female (Scotland). *(C) Porcellidium fimbriatum* Claus, 1863, female (Scotland). *(D)* Male *P. viride*. *(E)* Male *P. fimbriatum*. *(F) Porcelloides scutatus* (Claus, 1889) female (Ireland). *(G) Porcelloides tenuicaudus* (Claus, 1860) female (Scotland). Scale bar: 0.4 mm.

—— Ventral blade slightly more than ½ length of segments 3+4, large thorn-like spine ventral to δ seta. P1 endopod with band of minute setules down medial edge and smaller area on lateral edge. Distance between T3 and T4 on female CR = 10% of CR width, T1 = T4 in length. Body length, male 0.46 mm, female 0.61 mm. Female CR/L = 9%, CR l/w = 1.4, H.I. for β = 15%, GDS cleft with lateral notch. [Original description incomplete]. S. Africa ..... *P. algoense* Hicks, 1982

—— Ventral blade as long as segments 3+4, talon-shape*. Ventral seta on male P5 baseoendopod 95% of exopod length. Female CR seta T4 > twice length of T1, distance between T3 and T4 25% of ramus width, Body length male 0.61 mm, female 0.69 mm. Female body L/W = 1.6, CR/L = 11%, CR l/w = 1.5, H.I. for β = 23%, GDS w/l = 1.4. Ruby red. Argentina, Tristan da Cunha ..... *P. rubrum* Pallares, 1966

—— Ventral blade present*. Ventral seta on male P5 baseoendopod 40% of exopod length. Female T1 = T4 in length, distance between T3 and T4 10% of ramus width. Body length male 0.55 mm, female 0.76 mm, female body L/W = 1.7, CR/L = 11%, CR l/w = 1.8, H.I. for β = 15%, GDS w/l = 1.3. Red-brown. SW. Africa ..... *P. hartmannorum* Tiemann, 1978

3 First seta on male antennule segment 2 > twice length of setae 2 and 3, five plumulose setae on segment 2, denticles on segment 4 denticulate pads (Fig. 7A). Male P5 almost rectangular, apical angle 75°. Body length male 0.62 mm, female 0.91 mm, CR/L = 15%, CR l/w 2.3, H.I. for β = 50%. Border of boundary between anterior and posterior lobes of GDS marked by a clear area without dorsal pits or border setules. Large serrated seta on P3 1.4 times length of endopod. Colourless with variable pattern of dark blue/purple areas. Europe. (Plate 1B,D, p. 67) ..... *P. viride* (Philippi, 1840)

—— First seta on male antennule segment 2 same length as setae 2 and 3, no plumulose setae on segment 2. Ventral surface of male rostrum with U-shaped ridges (Fig. 14F). Male P5 trapezoid, apical angle 40°. Body length male 0.70 mm, female 0.85 mm, CR/L = 14%, CR l/w 2.4, H.I. for β = 16%. GDS with slight indentation without setules. Dorsal surface of CR with pits. Large serrated seta on P3 1.4 × length of endopod. Europe ..... *P. roscoffensis* (Bocquet, 1948)

—— First seta on male antennule segment 2 same length as setae 2 and 3, no plumulose setae on segment 2, first denticle on segment 4 finger-like with serrulate edge, segment 5 expanded laterally. Hyaline border of cephalosome striated. Female rostrum obscured by anterior bulge of cephalosome. Body length male 0.69 mm, female 0.84 mm, CR/L = 8%, CR l/w = 1.95, H.I. for β = 33%. GDS with notch. Large serrated seta on P3 short, 1.1 times length of endopod. Yellow with red dorsal stripe. Japan. (Plate 2G, p. 69) ..... *P. akashimum* Harris & Iwasaki, 1996

4 P1 endopod segment 1 with band of minute setules down medial edge (Fig. 2E) 5

—— P1 endopod segment 1 without any minute setules down medial edge 6

5 Female body elongate, length to width ratio = 2.18, cephalosome width/rostrum = 3.3. Male antennule segment 4 denticle 1 pointed with serrulations along both edges, denticle 2 tooth-like, 3 with serrulate edge. Body length male 0.57 mm, female 0.72 mm, CR/L = 6.5%, CR l/w = 1.25, H.I. for β = 7.7%, GDS width/length = 1.25, arch 26% of length. Amber colour. Australia. (Plate 2E, p. 69) ..... *P. naviculum* Harris & Robertson, 1994

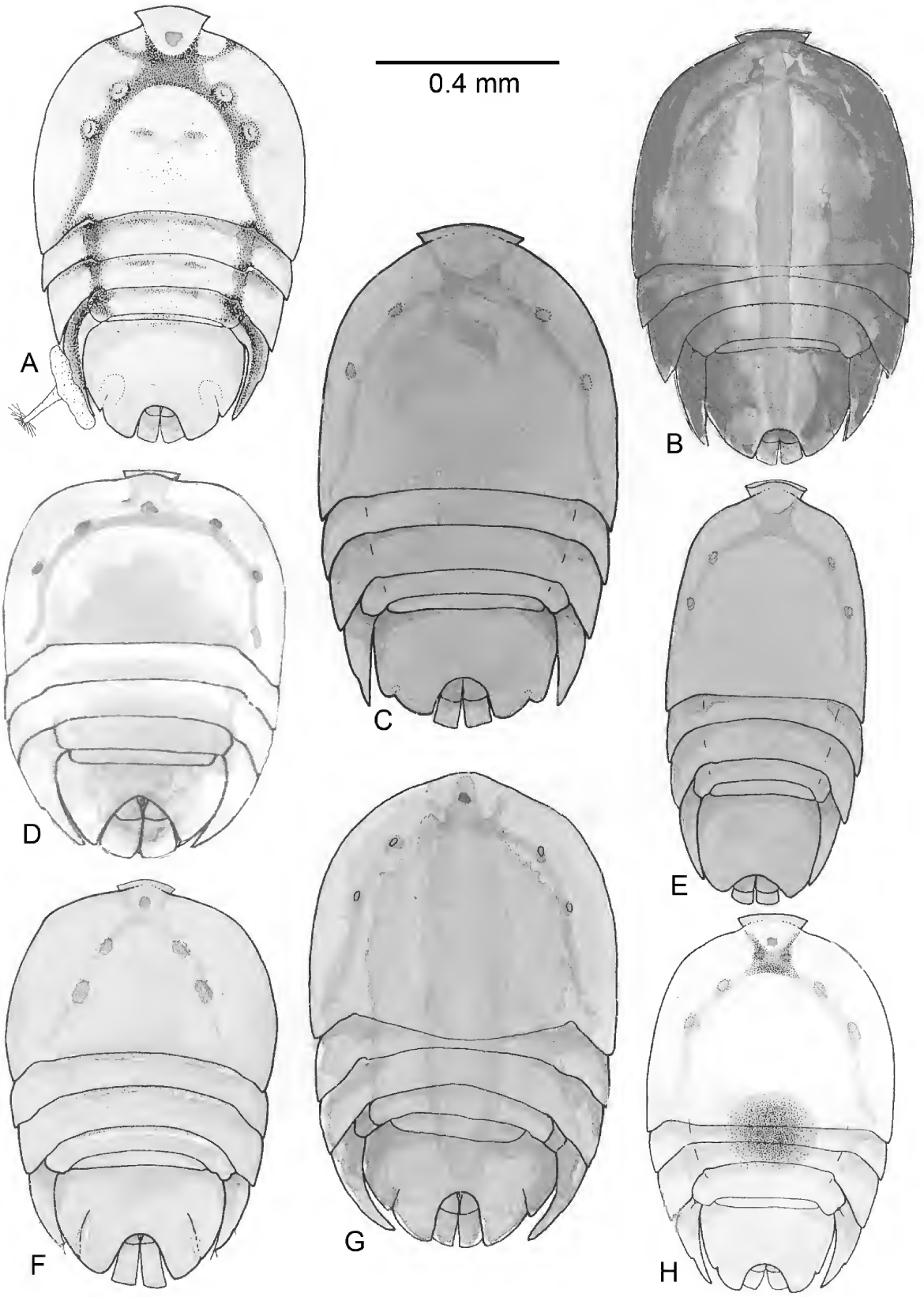

Plate 2. *(A) Porcellidium erythrogastrum* Harris & Robertson, 1994, female (Australia). *(B) P. pulchrum* Harris & Robertson, 1994, female (Australia). *(C) P. phyllosporum* Harris & Robertson, 1994, female (Australia). *(D) P. wandoensis* Kim & Kim, 1997, female (Korea and Japan). *(E) P. naviculum* Harris & Robertson, 1994, female (Australia). *(F) P. londonarum* Harris, 1994, female (Australia). *(G) P. akashimum* Harris & Iwasaki, 1996, female (Japan). *(H) P. ocellum* Harris & Robertson, 1994, female (Australia). Scale bar: 0.4 mm.

—— Female body broad oval, length to width ratio = 1.7, rostrum very broad, cephalosome width/rostrum = 2.8. Male antennule segment 2 triangular, denticle 1 on segment 4 C-shaped. Body length male 0.73 mm, female 0.93 mm, CR/L = 5.8%, CR l/w = 1.05, H.I. for β = 25%, GDS very broad width/length = 1.6, arch 20% of length. Orange brown colour. Australia. (Plate 2C, p. 69) ..... *P. phyllosporum* Harris & Robertson, 1994

—— Large lateral area of fine setules on P1 endopod. Female rostrum (Fig. 1I) a horizontal bar in ventral view (not triangular), not broad, cephalosome width/rostrum = 4.48. Denticle 1 on segment 4 of male antennule with serrate edge, 2 small with lateral serrulation, 3 long, tooth-like. Body length male 0.54 mm, female 0.79 mm, CR/L = 11%, CR l/w = 2.4, H.I. for β = 14. GDS width/length = 1.5. Colour pale yellow. Australia. (Plate 1A, p. 67) ..... *P. rastellum* sp. nov.

—— Ventral blade absent* Small lateral area of fine setules on P1 endopod. Female P5 very broad, internal seta on baseoendopod very long, 85% of falciform ridge. Large serrated seta on P3 very long, 1.7 times length of endopod. Body length* male 0.48 mm, female 0.57 mm, CR/L = 5.5%, CR l/w = 1.4, GDS w/l = 1.34. Colour blood red. Aeotearoa (New Zealand) ..... *P. erythrum* Hicks, 1971

6 First denticle on male antennule segment 4 pointed, comb-like, 2 and 3 rounded denticulate or serrulate 7

—— Denticles on male antennule segment 4 swollen or bulbous (not serrated or denticulate) 10

7 GDS arch short, arch height/width 0.9, arch height/GDS length = 35% 8

—— GDS arch high, arch height/width > 0.9, arch height/GDS length = > 40% 9

8 First denticle on male antennule pointed, 2 and 3 rounded serrulate. Body length male 0.63 mm, female length 0.73 mm, width/rostrum = 3.9, CR/L = 8.2%, CR l/w = 1.75, H.I. for β = 26%. Arch height 30% of GDS length, arch height/width = 0.7. Korea, Japan ..... *P. brevicavum* Kim & Kim, 1997

9 First denticle on male antennule segment 4 pointed, comb-like, 2 and 3 denticulate pads, spine attached to anterior lobe at base of δ seta. Body length male 0.68 mm, female 0.94 mm, cephalosome width/rostrum = 4.2, CR/L = 11%, CR l/w = 2.4, H.I. for β = 40%. Arch height 45% of GDS length, arch height/width = 1.1. Colour orange brown. Japan, Korea ..... *P. ofunatense* Harris & Iwasaki, 1996

—— First denticle on male antennule segment 4 pointed, comb-like, 2 and 3 small denticulate pads, no spine attached to anterior lobe. Body length male 0.58 mm, female 0.81 mm, cephalosome width/rostrum = 3.6, CR/L = 10.5%, CR l/w = 2.6, H.I. for β = 41%. Arch height 45% of GDS length, arch height/width = 1.2. Bright yellow. Japan ..... *P. kiiroum* Harris & Iwasaki, 1996

10 Denticles on segment 4 of male antennule bulbous (rounded) with feint serrulation unlike the typical pointed, tooth-like or denticulate pad of other species), short thick seta at base of anterior lobe, unique pinnate seta anterior to the first denticle on segment 4. Body length male 0.61 mm, female 0.76 mm, CR/L = 17%, CR l/w = 2.1, H.I. for β = 40–45%. Colour pale blue or pale brown with blue edge. Korea, Japan. (Plate 2D, p. 69) ..... *P. wandoensis* Kim & Kim, 1997

Notes: In doubtful cases, identification should be confirmed by reference to original description where details of the male antennule will be found.

Remarks. The above generic diagnosis is based on animals collected from Oban Scotland and identified as *Porcellidium viride* from Brady's (1880) illustration which shows a species specific character of the male antennule. Brady collected specimens from the same region of Scotland.

Fifty-nine species of *Porcellidium* have been named in the literature, but 18 of these cannot be counted as valid species for the following reasons. Seven names are synonyms for other species i.e., *P. dentatum,* and *P. ovatum* for *Porcelloides tenuicaudus*; *P. lecanoides* and *P. sarsi* for *P. viride*; *P. penicilliferum* for *Dilatatiocauda tristanensis*; *P. acutum* for *Kensakia acuta*; and *P. aoifuchidorum* for *P. wandoensis*, three are given to juvenile stages (*subrotundum, rotundum, australe*) and another eight species cannot be identified or placed in a genus because the original description is devoid of specific characters, (*P. fulvum, P. interruptum, P. tuberculatum, P. affine, P. charcoti, P. wolfendeni, P. scotti,* and *P. malleatum*), however, some of these may prove to be valid species if redescribed in detail.

This leaves 41 species sufficiently well described to be identified and assigned to a genus, though only 20 of these can be assigned to *Porcellidium* on the diagnosis given above. The remaining 21 species possess apomorphic characters that exclude them from *Porcellidium* and must be transferred to other genera within the Porcellidiidae.

The genus *Porcellidium* is not based on apomorphies, but on a combination of characters all of which may be found in other genera either in an apomorphic or plesiomorphic state.

Porcellidium rastellum sp. nov.

Figs 1–3

Type material. Holotype adult male, length 0.55 mm, P81207; allotype adult female, length 0.80 mm, P81208, collected from *Sargassum* sp., sublittoral, Pontoon Rocks, Ballina, NSW, Australia, (28°52'S 153°36'E), V. A. Harris, 1982. Paratype specimens P81209 (20 ♀♀, 10 ♂♂, 10 ♂♂ + juvenile) and paratypes P88552, P88553, P88554, all deposited at AM, Sydney. Specimens from the type series and Cronulla, Sydney (50 ♀♀, 30 ♂♂ + 50 ♂♂ coupled to juv. ♀), deposited at NHM, London.

Diagnosis. Female rostrum horizontal bar, (in ventral view not V-shaped (Fig. 1I), anterior edge of cephalosome folded ventrally (Fig. 1D), hyaline border not modified; maxilla with conspicuous rake-like claw (Fig. 2G); P1 exopod segment 1 with conspicuous crescent of denticulate setules, endopod with extensive lateral and medial peg areas consisting of minute denticles arranged in rows (Fig. 2E); male antennule first seta on segment 2 same length as second seta, no plumulose setae on segment 2, segment 3 without ventral process, three denticles on segment 4 none are denticulate pads; female P5 with broad medial dorsal expansion (Fig. 1C). Spermatophore elongate, ephemeral on female.

Biometric data. *Females* (N = 15): maximum length (L_{max}) 0.79 mm, range 0.76–0.81 mm, body length to end of genital double-somite (L_{urs}) 0.77 mm, range 0.74–0.81 mm; cephalosome width (W) 0.55 mm, range 0.54–0.56 mm; rostrum width (R) 0.12 mm; genital double-somite width 0.28 mm, length 0.19 mm, arch 0.9 mm; caudal ramus length 0.12 mm, width 0.05 mm.

Ratios: L_{urs}/W 1.41; W/R 4.6; genital double-somite w/l 1.5; caudal ramus 15% of L_{urs}, ramus, l/w 2.4, Hicks' index for α 72%, for β 14%.

Males (N = 9): maximum length (L_{max}) 0.55 mm, body length (L_{urs}) 0.54 mm; cephalosome width 0.45 mm; antennule length 0.135 mm.

Ratios: L_{urs}/W 1.2; antennule 30% of L_{urs}; segment 2 30%, segment 3+4 46% and dactylus 23% of antennule length.

Description. *Adult females* (Fig. 1A; Plate 1A, p. 67): colour pale yellow, rostrum a horizontal bar in ventral view (Fig. 1I, not V-shape), wide (W/R = 4.2). The anterolateral edge of the cephalosome and hyaline border is folded ventrally as far as the second border sensillum, but without modification in structure (Fig. 1D), hyaline border 8–10 µm wide, granular in appearance. Dorsal pits are conspicuous, very few dorsal sensilla. Labrum without ridge plates. Genital double-somite (Fig. 1F) bordered with strong setules, dorsal surface pitted, anterior and posterior lobes separated by deep notch, posterior lobe rounded, arch about half length of genital double-somite. Caudal rami rectangular (Fig. 1E), dorsal surface with pits, no setules on medial or lateral edges, terminal setae pinnate, T1 not recessed, T2 and T3 close together, T4 set in from medial corner which is slightly bevelled, β seta close to posterior border, fringe of setules on posterior edge between T3 and medial corner (Fig. 1H). Structure and setation of ambulatory limbs and mouthparts typical of family. Basis of antenna with oblique double row of setules (Fig. 2A), endopod segment 2 with three lateral setae, end part of geniculate setae plain, terminal claw comb-like. Mandible (Fig. 2F) with strong molar process, small group of setules on anterior lobe of palp, maxillule (Fig. 2C), maxilla endopod with conspicuous rake-like or ctenoid claw (Fig. 2G), maxilliped (Fig. 2B) normal. First ambulatory limb P1 with conspicuous crescent of rod-like denticles parallel to edge of exopod segment 1, endopod has broad band of denticles down medial edge and a large latero-central area of denticles which occupies nearly ¼ of the area anterior to the fimbriate crescent, denticles are minute and arranged in parallel rows, endopod l/w = 1.35 (Fig. 2E). Serrulate spinous seta on P2 endopod segment 3 almost as long as endopod (Fig. 3A). Serrate spinous seta on P3 endopod segment 2 (Fig. 2F) shorter than endopod (0.8:1), large serrate spinous seta on segment 3 much longer than endopod (1.4:1). P4 endopod segments 2 with straight serrulate spinous seta, serrulate spinous seta on segment 3 J-shape (Fig. 3B). Ventral seta on baseoendopod of P5 reaches back to level of lateral seta on exopod, P5 exopod (Fig. 1C) lanceolate with broad dorsal medial expansion which partly covers genital double-somite (Fig. 1A, C), there are two sub-apical dorsal setae and one short apical seta, dorsal surface of P5 pitted. Females carry eight or 10 eggs in brood chamber.

Adult males (Fig. 1B) colour, dorsal pits and hyaline border as for female. Cephalosome truncated, shoulders smoothly rounded, lateral corner of antennule socket not prominent, anterior edge of cephalosome and hyaline border reflexed ventrally (as in female) but not modified. Dorsal surface of genital double-somite pitted. Caudal ramus (Fig. 1G, J) with bevelled medial corner makes ramus appear pentagonal, dorsal surface with pits. Setae as for female with β seta close to posterior border, T1 not recessed, T4 set in at base of bevelled medial corner, posterior fringe of setules extends past T4 along bevelled edge. Antennule (Fig. 2D) segment 2 short triangular without plumulose setae, first seta not longer than 1.5 times other setae on segment, no ventral process or blade on segment 3, segment 4 with three coupling

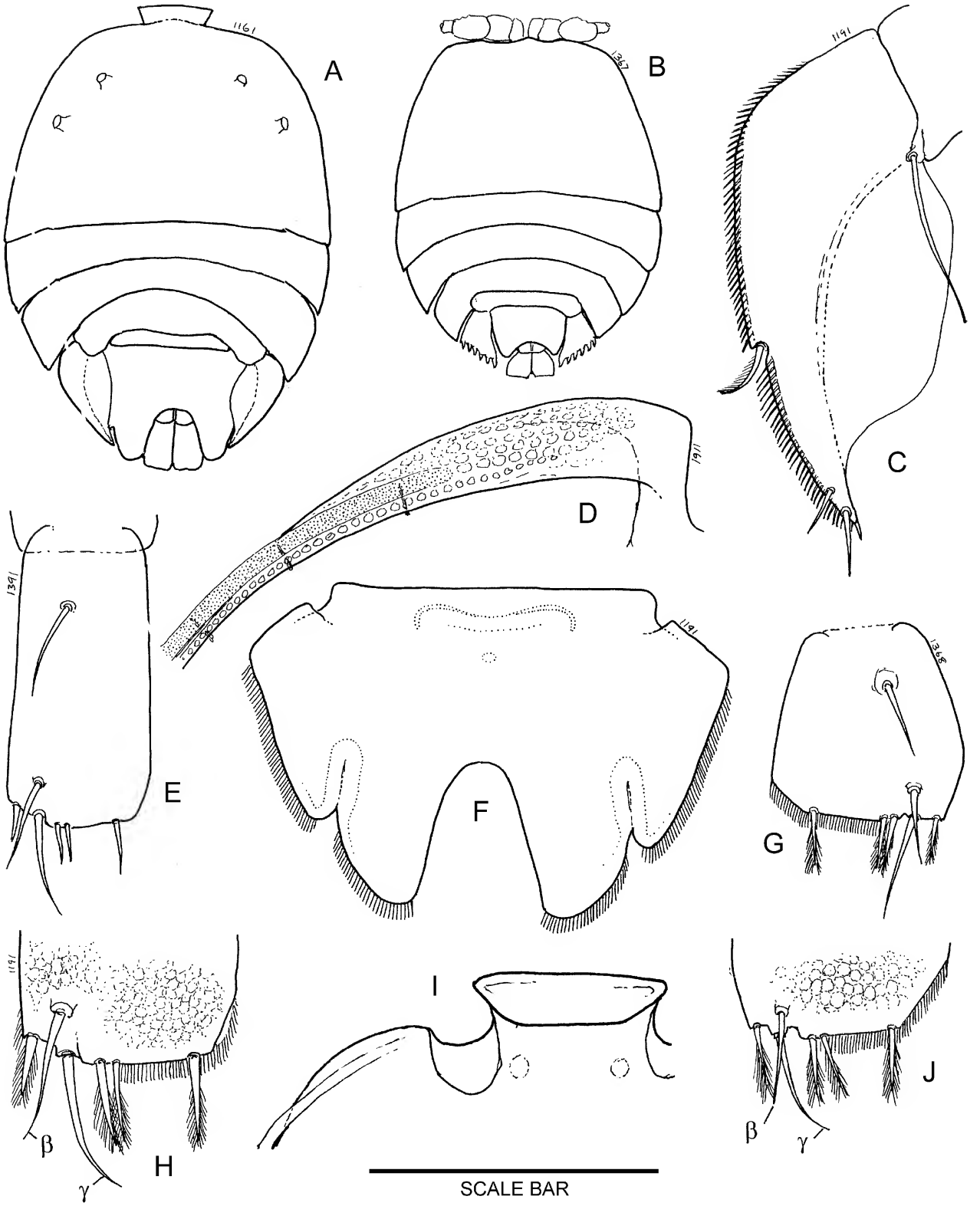

Figure 1. *Porcellidium rastellum* sp. nov. Female: *(A)* adult; *(C)* P5 (ventral); *(D)* anterior edge of cephalosome showing folded edge (ventral); *(E, H)* caudal ramus; *(F)* genital double-somite; *(I)* rostrum (ventral). Male: *(B)* adult; *(G, J)* caudal ramus. Scale bar: A, B, = 0.52 mm. C, D, G = 0.09 mm. E = 0.12 mm. F, I = 0.17 mm. H, J = 0.06 mm.

denticles, dactylus short, broad, segment 6 very small. Remaining limbs as for female except that P2 endopod has only two terminal setae (Fig. 3D) and setae on P4 endopod segments 2 and 3 are not spinous (Fig. 3E). P5 trapezoid with ventral row of setules to lateral seta but no setules at base of terminal setae, dorsal surface pitted (Fig. 3C).

Etymology. The specific name refers to the rake-like claw on the maxilla, (L. *rastellum* = a small rake Fig. 2G).

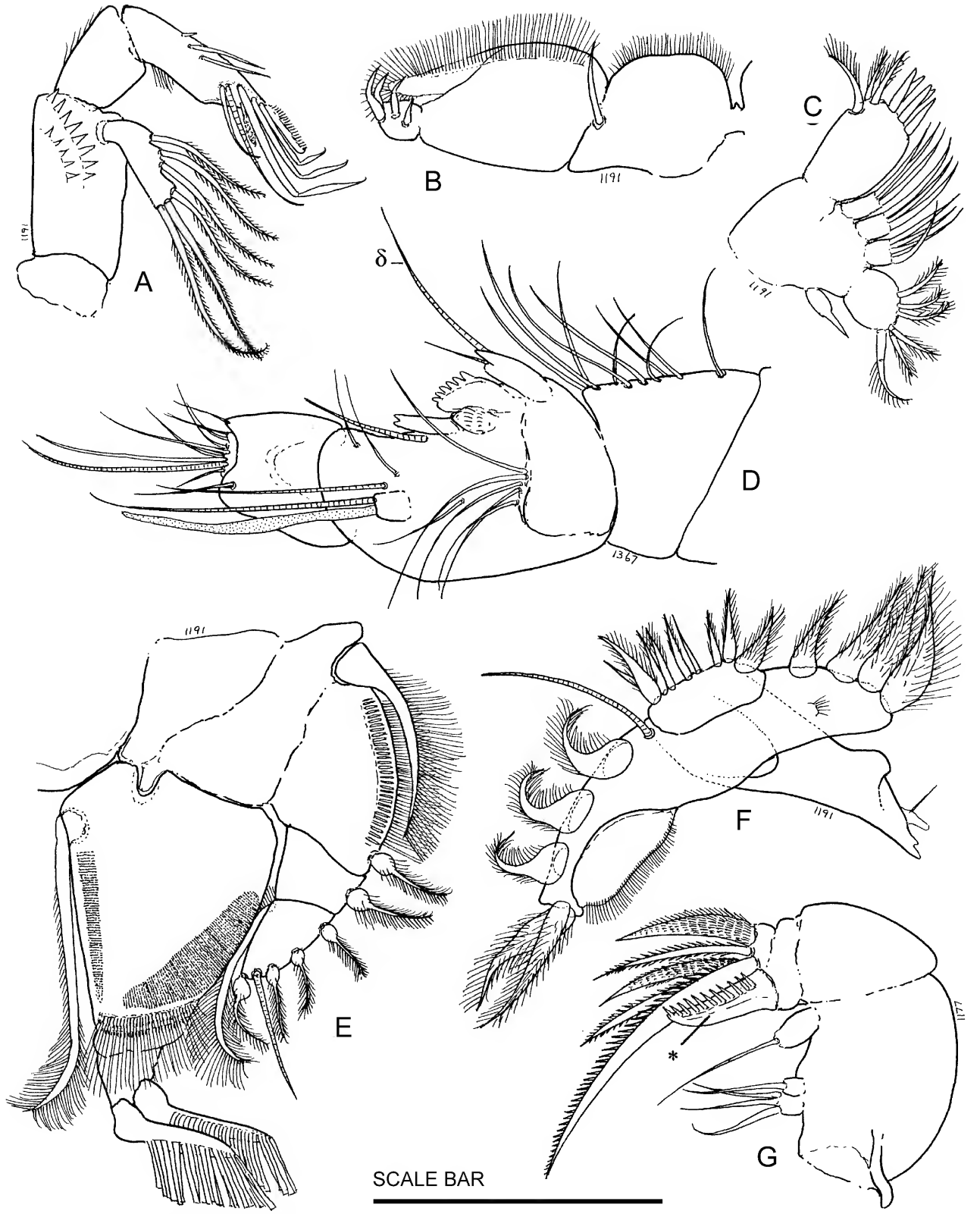

Figure 2. *Porcellidium rastellum* sp. nov. Female: *(A)* antenna; *(B)* maxilliped; *(C)* maxillule; *(E)* P1; *(F)* mandible; *(G)* maxilla (*rake-like claw on endopod). Male: *(D)* antennule. Scale bar: A, B, E, F = 0.12 mm. C, D, G = 0.06 mm.

Remarks. *Porcellidium rastellum* differs from most other members of the genus in the large areas of very small denticles that appear to be arranged in rows on the ventral (anterior) surface of the P1 endopod. Another unusual feature is the way in which the anterior part of the cephalosome border is folded ventrally. This results in a portion of the hyaline border lying in a ventral position. However, this does not correspond to the condition in *Tectacingulum* because there is no modification of the hyaline border and only the anterior part of the border is reflexed.

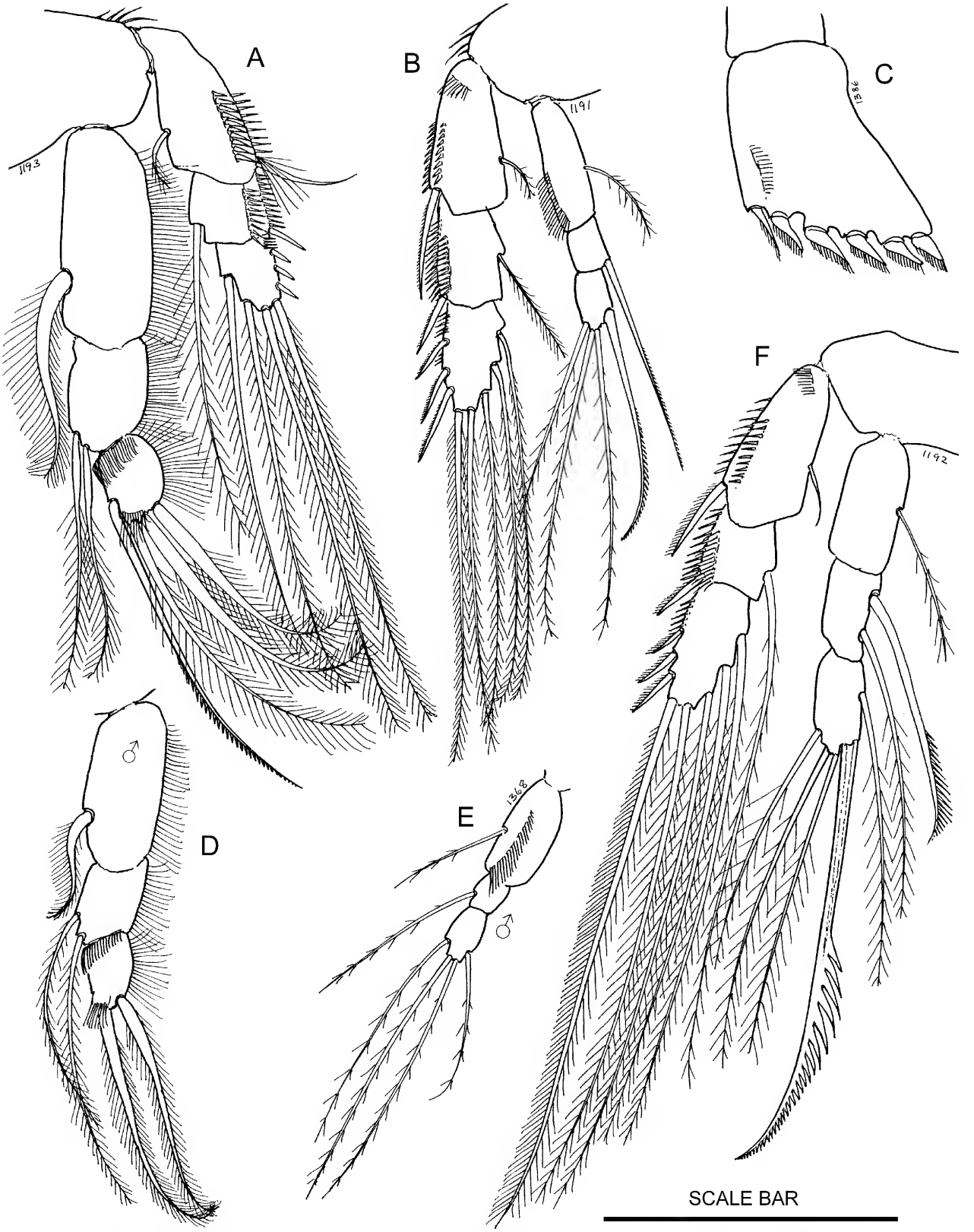

Figure 3. *Porcellidium rastellum* sp. nov. Female: *(A)* P2; *(B)* P4; *(F)* P3. Male: *(C)* P5; *(D)* P2 endopod; *(E)* P4 endopod. Scale bar: A–F = 0.09 mm.

Distribution. The species has been recorded as abundant on several algal species from Nambucca, northern NSW (30°37'S) to Broulee (35°52'S), but not from Hervey Bay, Queensland (25°15'S) or Eden, southern NSW (37°06'S). Collected from *Sargassum* sp., Ballina, Bal12.11/82, 162 ♀♀, 44 ♂♂ + 90 ♂♂ coupled to juvenile female: Nambucca, Nb6.11/82, 141 ♀♀, 160 ♂♂ mostly coupled. *Rhodymenia*? Type series,Ballina, Bal14.11/82, 225 ♀♀, 176 ♂♂. *Lobophora* sp., Cronulla, Sydney, Cr19.8/75: Cr33.2/77, 100+, V. A. Harris 1975, 1977, 1982.

Porcellidium viride (Philippi, 1840)

Figs 4–8

Thyone viridis Philippi, 1840:190, pl. IV, fig 2.
Porcellidium subrotundum Norman, 1868.—Brady, 1880: 169–170.
Porcellidium lecanoides Claus, 1889.—Holmes & O'Connor, 1990: 66; Huys *et al*., 1996: 308; Walker-Smith, 2001: 656; Wells, 2007:79.
Porcellidium viride.—Brady, 1880: 168–169; Lang, 1948: 420–422; Apostanov & Marinov, 1988: 101–102; Harris & Robertson, 1994: 301; Bodin, 1997: 65.
Porcellidium fimbriatum Claus, 1889.—Brady, 1880 (female): 167; Thompson & Scott, 1903: 227; Sars, 1904: 76–77.
P. fimbriatum var. *heraldicum*.—Monard, 1928: 324–326; Monard, 1935.
Porcellidium sarsi.—Bocquet, 1948: 237–259; Holmes & O'Connor, 1990: 66–67; Harris & Robertson, 1994: 301; Huys *et al*., 1996: 308; Walker-Smith, 2001: 656; Wells, 2007: 79.
Thyone viridis Philippi.—Vervoort, 1964: 119.

Type material. Due to the apparent absence of a type specimen for Philippi's *Thyone viridis*, a male specimen, (identified as *Porcellidium viride* from Brady's illustration of the antennule) is here designated NEOTYPE to give taxonomic stability to the genus *Porcellidium* and to allow sufficient definition of the specific characteristics to ensure recognition of *Porcellidium viride*.

Neotype designation. NEOTYPE adult male with antennules extended, length 0.63 mm, P90778 deposited at the Australian Museum, Sydney; collected from *Laminaria digitata*, Clachan, Seil Sound, Oban, Scotland (56°19'N 5°35'W), V.A. Harris 1997.

Material examined (specimens here determined to be conspecific with the neotype): an adult female with egg mass detached, length 0.92 mm (AM P90779) and other specimens (20 ♀♀, 8 ♂♂ and coupled ♂ + juv. ♀, AM P89054), deposited at AM, Sydney. Specimens from the same locality and species of seaweed (100 ♀♀, 50 ♂♂ and 6 ♂♂ + juv. ♀, and 4 slide mounted specimens) have been deposited at NHM, London. Slide material in NHM, London (*Porcellidium* 339) and NMI, Dublin (see Appendix 1 and 2). Living material, identified as *Porcellidium viride* from a species specific feature of the male antennule shown in Brady's (1880) illustration, was collected from Castle Head, Dale, Pembrokeshire (51°42'N 5°10'W), Clachan, Seil Sound, Oban, Scotland (56°19'N 5°35'W) and Loch Hyne, Co. Cork, Ireland (51°30'N 9°17'W) and is part of the material examined. The following description is based on the neotype and this material examined.

Diagnosis. Male antennule segment 2 with first (proximal) seta more than twice length of second or third seta, five setae on segment 2 finely plumulose, segment 3 with ventral process or "peg", three coupling denticles on segment 4 are conspicuous denticulate pads, dactylus (segment 5) expanded, hooked distally, segment 6 inconspicuous; ventral surface of male rostrum smooth, no U-shaped wrinkles or ridges, ventral surface of female rostrum V-shape (Fig, 6F); female caudal ramus rectangular, l/w = 2, terminal setae T2 and T3 thin, plain, very close together, posterior border between setae T3 and T4 > ½ width of ramus, Hicks' index for β seta 45–50%; boundary between anterior and posterior lobes of female genital double-somite marked by a clear triangular area without border setules or dorsal pits, border of posterior lobe with three sensilla at edge; male P5 exopod almost rectangular, posterior angle 80°; females carry 24 eggs. Spermatophore elongate, ephemeral on female.

Biometric data. *Females* (N = 50): maximum length (L_{max}) 0.91 mm, body length to end of genital double-somite (L_{urs}) 0.89 mm, range 0.83–0.95 mm; cephalosome width (W) 0.60 mm, range 0.56–0.62 mm; rostrum width (R) 0.15 mm; genital double-somite width (N = 5) 0.38 mm, length 0.26 mm; caudal ramus length (N = 15) 0.14 mm [ramus dissected, laid flat], width 0.06 mm.

Ratios: L_{urs}/W 1.48; W/R 4.0; genital double-somite 63% of cephalosome width, w/l 1.45; caudal ramus 16% of L_{urs}, l/w 2.3, Hicks' index for β seta 50%.

Males (N = 16): maximum length 0.62 mm, body length to end of genital segment 0.49 mm; cephalosome width 0.52 mm; antennule (N = 7, fully extended) 0.15 mm; apical angle of P5 75–80°; spermatophore length 0.21 mm.

Ratios: male antennule 30% of cephalosome width; antennule segment 2, 33%, segment 3+4 37%, dactylus 24% of antennule length; first seta on segment 2 of antennule is 2.5–2.8 times length of seta 2; spermatophore 43% of body length L_{urs}.

Description. *Adult females* (Fig. 4A; Plate 1B, p. 67): pale yellow or colourless with variable patches of dark blue/purple on cephalosome and posterior of body (see Figs 4A, 8A, F, G, H, I and *Remarks* below). Cephalosome semicircular, rostrum broad (w/l 4.2), V-shape in ventral view (Fig. 6F). Hyaline border with eight border sensilla surrounds cephalosome, 10 µm wide. Dorsal surface ornamented with circular pits 4–5 µm, surface ridge near antennule socket (Fig. 8B, C), ventral surface of cephalosome smooth (not wrinkled). Labrum with oval patch of minute setules (Fig. 4F). Genital double-somite (Fig. 4C) broad, semicircular in outline, no cleft or notch but clear triangular area without border setules or dorsal pits marks boundary between anterior and posterior lobes, three very small sensilla at edge of posterior lobe (Fig. 4D). Posterior arch deep (½ length of genital double-somite), encloses almost whole of caudal rami. Genital opening (Fig. 4E). Caudal rami (Fig. 4B) long, rectangular, feint ridges on dorsal surface, β seta half way down ramus, γ seta and pinnate T1 slightly recessed at lateral corner, T2 and T3 plain, slender, very close together (T2 pinnate on some specimens), space between T3 and T4 greater than half width of ramus, T4 pinnate at medial corner (Fig. 4G). Some of the setae on segment 2 of female antennule finely plumulose (Fig. 5A). Structure and setation of mouthparts and ambulatory limbs typical of family. Antenna (Fig. 5B), endopod segment 2 with two lateral setae, ends of geniculate setae plain, claw comb-like (Fig. 5C). No patch of setules on anterior lobe of mandibular palp (Fig. 5E). Maxillule (Fig. 5G) with single bulbous seta on exopod, six setae on endopod. Coxae of maxilliped meet in midline (Fig. 5H). Limb P1, endopod segment 1 triangular, broad (l/w = 0.95), peg area inconspicuous (Fig. 5F). Serrulate spinous seta on segment 2 of P3 endopod (Fig. 6G) almost as long as endopod (0.9:1), large serrate spinous terminal seta on segment 3 longer than endopod (1.4:1). Spinous setae on P4 endopod segment 2 and 3 (Fig. 6C) longer than endopod (1.3:1). P5 exopod lanceolate with two plain dorsal setae (one sub-terminal and one apical), minute third seta present on some specimens (Fig. 6H). Females carry 24 eggs per brood.

Adult males (Fig. 8A; Plate 1D, p. 67). Dark blue/purple area only on cephalosome, posterior of body colourless. Cephalosome truncated, anterior border straight, shoulder

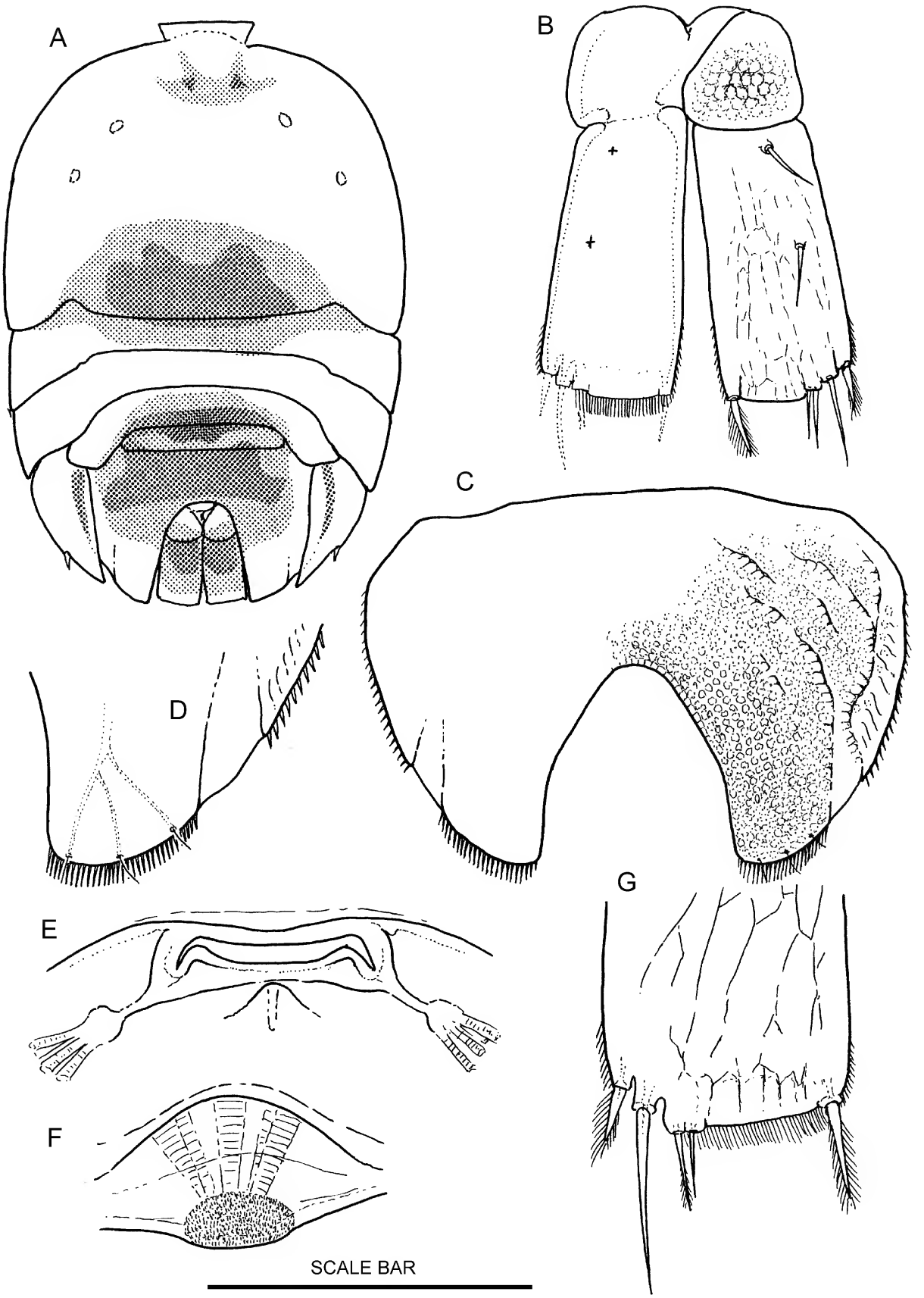

Figure 4. *Porcellidium viride* (Philippi, 1840). Female: *(A)* adult showing typical colour pattern; *(B)* caudal rami (left ventral, right dorsal); *(C)* genital double-somite; *(D)* detail of genital double-somite posterior lobe; *(E)* genital opening; *(F)* labrum; *(G)* caudal ramus, terminal setae. Drawings of specimens from Scotland. Scale bar: A = 0.5 mm. B = 0.15 mm. C = 0.23 mm. E, F = 0.13 mm. G = 0.08 mm.

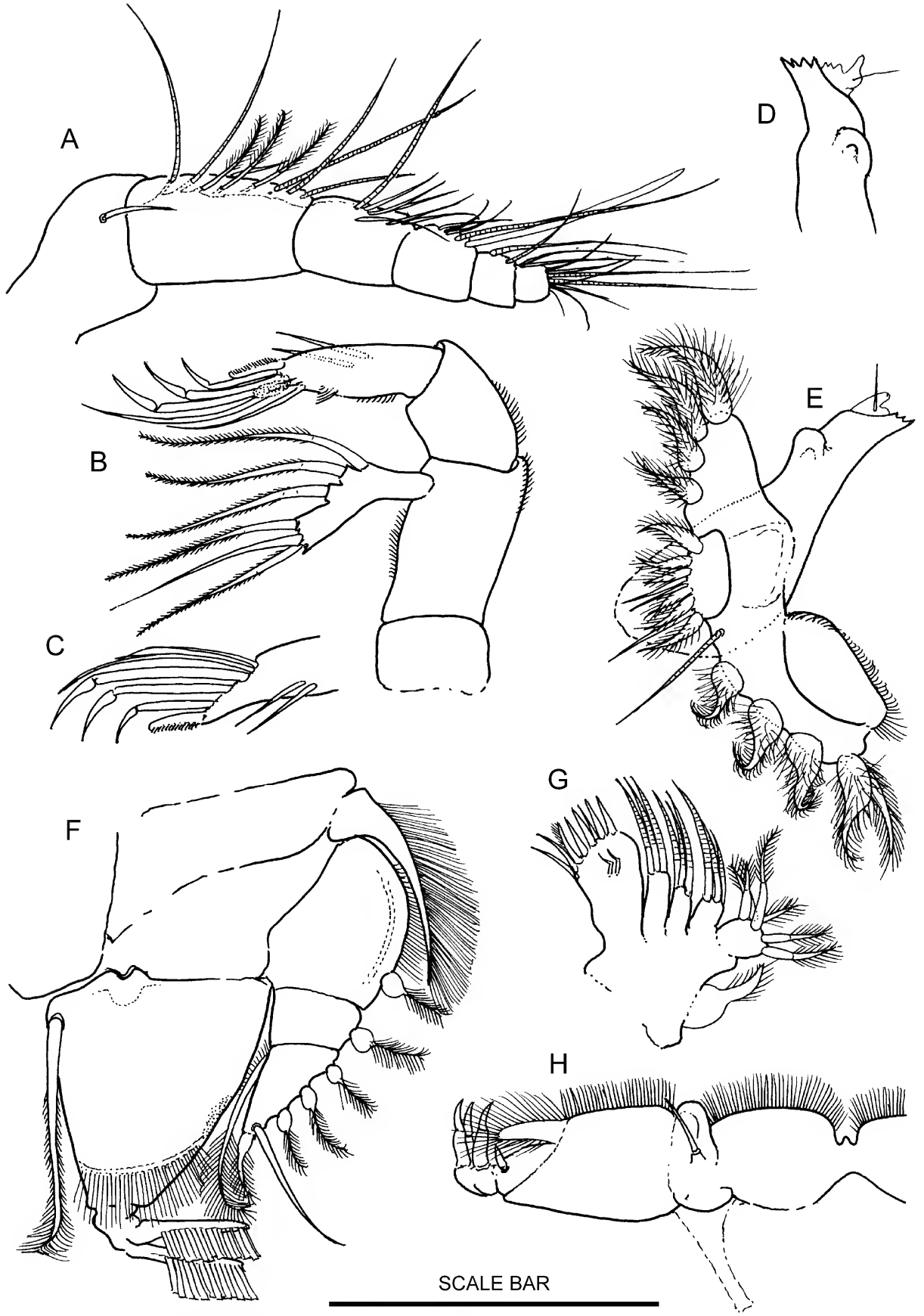

Figure 5. *Porcellidium viride* (Philippi, 1840). Female: *(A)* antennule; *(B, C)* antenna; *(D, E)* mandible; *(F)* P1; *(G)* maxillule; *(H)* maxilliped. Scale bar: A, B, G, H = 0.08 mm. E, F = 0.13 mm.

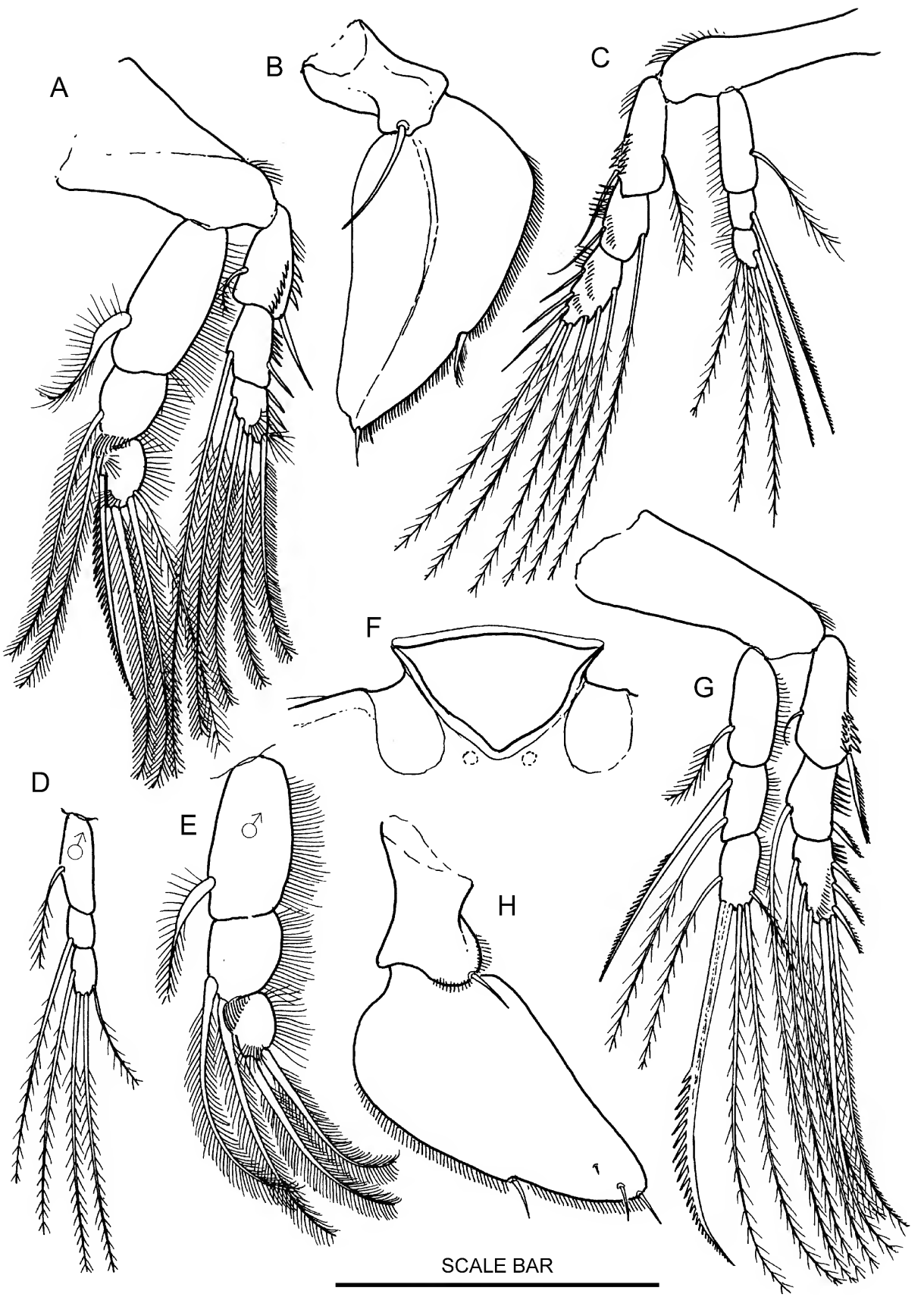

Figure 6. *Porcellidium viride* (Philippi, 1840). Female: *(A)* P2; *(B,H)* P5 (ventral and dorsal); *(C)* P4; *(G)* P3; *(F)* rostrum (ventral). Male: *(D)* P4 endopod. *(E)* P2 endopod. Scale bar: A, C, G = 0.18 mm. B, F, H = 0.23 mm. D, E = 0.15 mm.

Figure 7. *Porcellidium viride* (Philippi, 1840). Male: *(A)* detail of antennule coupling denticles; *(B, C)* P5 (ventral); *(D)* maxilla; *(F, G)* antennule (* peg or ventral process). Female: *(E)* showing extent of colour pattern of specimens from Loch Hyne, Ireland. Scale bar: A = 0.06 mm. B, D, F, G = 0.08 mm.

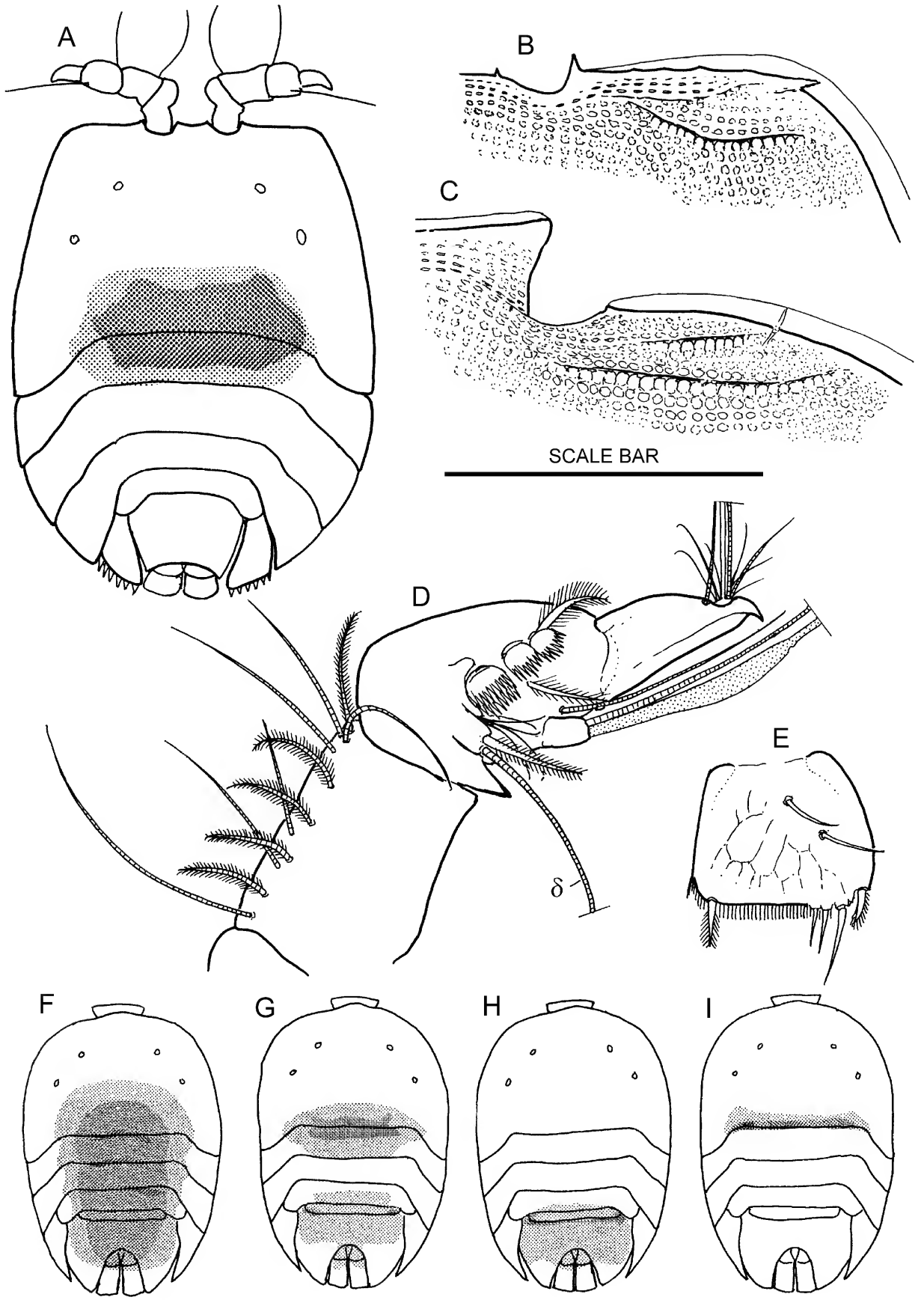

Figure 8. *Porcellidium viride* (Philippi, 1840). Male: *(A)* adult showing typical colour pattern; *(B)* anterior cephalosome (dorsal); *(D)* antennule (anterior); *(E)* caudal ramus. Female: *(C)* anterior cephalosome (dorsal); *(F, G, H, I)* colour patterns (see text). Scale bar: A = 0.45 mm. B, C = 0.13 mm. D, E = 0.08 mm.

tightly rounded. Hyaline border, dorsal pits and ventral surface of cephalosome as for female, no ridges or wrinkles on ventral surface of rostrum. Caudal ramus sub-quadrate (l/w 0.75), medial edge straight, lateral edge convex, dorsal surface with feint ridges, β seta ½ way down ramus (Fig. 8E). First seta on antennule segment 2 more than twice length of second and third seta (Figs 7G), five plumulose setae on segment 2. Segment 3 with knob-like ventral process (no blade). Segment 4 with three conspicuous denticulate coupling denticles, (in some views they may appear as two denticulate pads, compare Figs 7A and 8D). Aesthetasc short (more than twice length of segment 3+4). Segment 5 of dactylus broad, ¾ length of segments 3+4, hooked terminally, segment 6 very small, fused to segment 5 (Fig. 7F). Other limbs as for female except for the following: P2 endopod with two plumose terminal setae (Fig. 6E), setae on segments 2 and 3 of P4 endopod all plumose (Fig. 6D), P5 rhomboid (almost rectangular, Figs 7B, C), first (lateral) seta longer than other setae, no setules at base of terminal setae, apical angle of P5 80°. Spermatophore ⅓ body length.

Remarks. Although Brady's *Porcellidium viride* can be identified, the same does not apply to Philippi's *Thyone viridis*. The reason Brady thought his animal was the same as Philippi's *Thyone viridis* is the similarity of the P5 limbs. He says "There seems little reason to doubt the identity of this species [*P. viride*] with Philippi's *Thyone viridis*; the serration of the lower border of the fifth foot is very distinctive… ", but this is a feature of nearly all male members of the Porcellidiidae. It may seem strange that Brady thought his animals the same as Philippi's, but it is clear from his description and figure that he thought his own copepodid was an adult female. Brady had found *P. tenuicauda* (which he illustrates), and the adult female of *P. viride* which he identifies as *P. fimbriatum*, thus the only other animal he could compare with his (male) copepodid was *Thyone viridis*. It is important, therefore, to consider whether Brady's synonymy is justified.

Philippi gave a short (Latin) diagnosis of *Thyone* and then an extremely brief description of his *T. viridis*, "Almost ¾" long, common. Masticatory apparatus extremely complicated". The only clue to the animal's identity is a confusing sketch (Fig, 25A). It shows an animal with six segments to its antennule, but they are not transformed like an adult male members of the Porcellidiidae. This tells us that it is not an adult male or male copepodid: it must be an adult female. But the posterior end of the body clearly shows male P5 limbs with six terminal setae and quadrate caudal rami, therefore Philippi's animal must be a sage IV or V male copepodid. Thus there is a conflict as to the sex of the animal.

The shape of the body is even more confusing (see Fig. 24A). It is egg-shaped and sharply truncated anteriorly with maximum width ⅓ down body. Adult animals of Claus' *P. tenuicauda* are egg-shaped, but neither male nor female is truncated anteriorly. The males of both *P. viride* and *P. fimbriatum* are truncated anteriorly, but are not egg-shaped nor do they taper posteriorly. The females of these two species are oval and not truncated anteriorly. The copepodid of *P. viride* illustrated by Brady (1880) is not egg-shaped; the posterior half is broadly semicircular like other copepodids (Fig. 25B). It is clear that Philippi's animal cannot be identified with any of the European species nor can Brady be justified in thinking it was the same as his animal. Philippi does not say whether he designated type specimens for his animal and no evidence has been found that suggests he did. Brady would not have provided a type specimen for his *Porcellidium viride* because he regarded it as a synonym for *T. viridis*. However, Brady (1880) illustrates the male antennules of *P. viride* which show the unique long first seta on segment 2. This feature is species specific and has not been found on any other member of the family. It allows the species to be identified with a high degree of certainty and is the basis on which the present redescription of *Porcellidium viride* rests. Sars (1904) also shows this long seta in his illustration of *Porcellidium fimbriatum* which proves that his animals were *P. viride*.

Specimens from Wales and Scotland have a variable dorsal colour pattern of dark blue or purple on a pale yellow body colour (Figs 4A, 8F,G,H,I and Plate 1B,D, p. 67). The frequency of colour variability found in one sample is shown below (Table 1). Animals collected from Loch Hyne, Ireland, have a single pale pink dorsal patch (Fig. 4E).

Collection data. *Porcellidium viride* has been collected from the following algae. *Himanthalia elongata* at Great Castle Rocks, Dale, Pembrokeshire Wales, (CB7.7/70, 209 ♀♀, 88 ♂♂, 4 coupled ♂♂ + juvenile), V. A. Harris 1970, 1974. *Laminaria saccharina* at Clachan, Seil Sound, Oban, Scotland ES12.9/74, 71 ♀♀ (18 with eggs), 21 ♂♂, 4 ♂♂ coupled to juveniles; ES14.9/74, 14 ♀♀, 3 ♂♂; ES17.9/74, 85 ♀♀ (7 with eggs), 60 ♂♂, 13 ♂♂ coupled to juveniles; ES18.9/74 (holdfasts), 55 ♀♀, 12 ♂♂, 2 ♂♂ coupled to juveniles. *Laminaria digitata* at Clachan, Seil Sound, Oban, Scotland ES19.10/74, 55 ♀♀, 12 ♂♂; ES20.10/74, 58 ♀♀, 23 ♂♂; ES23.9/97, 41 ♀♀, 9 ♂♂; ES25.9/97, 55 ♀♀ (25 with eggs), 39 ♂♂, 2 ♂♂ coupled to juveniles, V. A. Harris 1970, 1974, 1987, 1997. *Ulva lactuca* at Loch Hyne, near Skibbereen, Co. Cork, Ireland LH3.9/97, 8 ♀♀, 6 ♂♂, V. A. Harris, 1997.

Samples collected from *Laminaria digitata* also contain populations of *P. fimbriatum*.

Table 1. Frequency of colour patterns in a population of *Porcellidium viride* from Scotland.

large purple area on all segments and posterior of body Fig. 8F	large purple patches on cephalosome Figs 4A, 8G	only posterior of body purple Fig. 8H	rear of cephalosome purple, posterior of body not purple Fig. 8A, I	animals pale yellow, no purple	total
female animals					
1	43	63	33	6	146
male animals					
0	0	0	104	2	106

Porcellidium fimbriatum Claus, 1863

Fig. 9–12

Porcellidium fimbriatum Claus, 1863:140, taf. xxii, fig. 1.
P. fimbriatum.—Claus, 1889: 32, figs. VII 1–18, VIII 1–8 (redescription); Bocquet, 1948: 247–250; Harris & Robertson, 1994: 301; Huys *et al.*, 1996: 308; Walker-Smith, 2001: 656; Wells, 2007: 79.
P. viride.—Lang, 1948: 420.
P. lecanoides.—Norman & Scott, 1906: 182.
Thyone viridis.—Vervoort, 1964: 119.

Type material. The description and illustrations Claus gave of *P. fimbriatum* (1863) are misleading for they do not show a single species specific character that would confirm the animal's identity. It is possible that Claus was looking at mixed material because, as shown above, *P. fimbriatum* and *P. viride* may be found in the same sample. In 1889 Claus redescribed his *P. fimbriatum* giving eight or more species specific characters which should have cleared up any misunderstanding between the two species, but his synonymies show that he believed his animals were the same species as Brady's *P. "fimbriatum"* which is known to be the female of *P. viride*. Moreover, *P. lecanoides* Claus, 1889 is a junior synonym for *P. viride*. In order to stabilize the taxonomy of *Porcellidium fimbriatum* in the apparent absence of a type specimen, a male with antennules extended to show species specific features has been selected as a NEOTYPE for *Porcellidium fimbriatum* Claus, 1863.

Neotype designation. NEOTYPE adult male with antennules extended, to show coupling denticles, length 0.56 mm, P92561 deposited at the Australian Museum, Sydney; collected from *Laminaria saccharina*, LW spring tide at Clachan, Seil Sound, Oban, Scotland (56°19'N 5°35'W), V. A. Harris, September 1997.

Material examined (specimens determined to be conspecific to the neotype): slide material in NHM (*Porcellidium* 339), (see Appendix 1); specimens from Castle Heads, Dale Pembrokeshire, Wales (51°42'N 5°10'W) and Clachan, Seil Sound, Oban, Scotland (56°19'N 5°35'W), identified as *P. fimbriatum* from Claus (1889); specimens collected from *Laminaria digitata* at Clachan, Scotland, AM P89055 (15 ♀♀, 8 ♂♂ + 3 coupled ♂♂, V. A. Harris, 1997). Other specimens (60 ♀♀, 30 ♂♂ + 8 coupled ♂♂, V. A. Harris, 1997) and slide mounted dissections have been deposited at NHM, London. The following description is based on the neotype and material examined.

Diagnosis. No finely plumulose setae on male antennule segment 2, first seta on segment 2 not longer than remaining setae, short blade-like ventral process on segment 3, three coupling denticles on segment 4 (proximal with serrated edge, two distal denticles small, botryoidal, no denticulate pad present), dactylus short (< ½ length of segment 4) segment 5 not expanded, segment 6 clearly visible, not fused to segment 5; no U-shaped wrinkles on ventral surface of male rostrum; female caudal ramus long, rectangular (l/w = 2.7–2.8), terminal setae T1–T4 all conspicuously pinnate, gap between T3 and T4 < ½ width of ramus, Hicks' index for β seta 25%; female genital double-somite with deep cleft or scar between anterior and posterior lobes (clear triangular area absent), no sensilla on border of posterior lobe; male genital segment with two rows of three dorsal sensilla; ventral surface of male and female cephalosome with fine lines (wrinkles); male P5 exopod trapezoid, apical angle 50°. Spermatophore elongate, ephemeral on female.

Biometric data. *Females* (N = 43): maximum length (L_{max}) 0.77 mm, body length (L_{urs}) 0.76 mm (range 0.73–0.79 mm); cephalosome width 0.45 mm (range 0.43–0.47 mm); rostrum (R) 0.095 mm; genital double-somite width 0.32 mm, length 0.27 mm; caudal ramus length 0.14 mm, width 0.05 mm.

Ratios: L_{urs}/W 1.7; W/R 4.7; genital double-somite width 70% of cephalosome width, w/l 1.2; caudal ramus 18% of L_{urs}, l/w 2.8, Hicks' index for β seta 25%.

Males (N = 25): maximum length (L_{max}) 0.56 mm, body length (L_{urs}) 0.50 mm; cephalosome width (W) 0.38 mm; spermatophore 0.15 × 0.03 mm; antennule fully extended 0.135 mm.

Ratios: L_{max}/W 1.47, L_{urs}/W 1.32; antennule 35% of cephalosome width, segment 2 30%, segment 3+4 42% and dactylus 15% of antennule length; spermatophore 27% of L_{urs}.

Description. *Adult females* (Fig. 9A; Plate 1C, p. 67): colourless or pale yellow with broad band of deep violet or dark blue down middle of back, including genital double-somite and caudal rami. Body outline elongate oval, sides of body almost parallel, rostrum narrow (W/R = 4.7). Dorsal surface of cephalosome, metasome and genital double-somite ornamented with dorsal pits (5–6 μm in diameter), ventral surface of cephalosome with fine wrinkles (see Fig. 12A). Hyaline border 8 μm wide. No patch of setules on labrum. Genital double-somite (Fig. 9H) relatively long (w/l = 1.2), posterior arch deep, slight notch or indentation between anterior and posterior lobes with transparent scar (scar appears as deep cleft when compressed with cover glass, *cf* Claus' 1889 illustration). No sensilla on edge of posterior lobe (Fig. 9E), border setules on posterior lobe longer than those on anterior lobe. Genital opening (Fig. 9G). Caudal rami (Fig. 9C, D) long (18% of body length), rectangular (l/w = 2.8), almost completely enclosed in arch of genital double-somite, dorsal surface with network of fine ridges but no pits. Medial edge straight, slightly bevelled distally, lateral edge slightly convex, both edges with setules posteriorly. Beta seta about ¾ down ramus (Hicks' index = 25%), terminal setae T1–T4 conspicuously pinnate, equal in length, T2 and T3 very close on slight prominence midway between T1 and T4, distance between T3 and T4 equal or less than ¼ width of ramus, very fine terminal fringe of setules between T3 and T4. No finely plumulose setae on segment 2 of antennule. Structure and setation of mouthparts and ambulatory limbs typical of family. Antenna (Fig. 10C). Mandible with small group of setules on anterior lobe of palp (Fig. 10B). Segment 1 of P1 endopod elongate triangular, narrow (l/w =1.5), coxa with internal seta (Fig. 10A inset). Serrulate spinous seta on segment 2 of P3 endopod (Fig. 11C) shorter than endopod (0.8:1), large serrate spinous seta on terminal segment considerably longer than endopod (1.7:1). P4 with internal serrulate spinous seta on segments 2 and 3 (Fig. 11A). P5 (Fig. 10F, G), exopod broadly lanceolate, with dorsal pits, one sub-terminal dorsal seta and two apical setae. Females carry 12–14 eggs per brood.

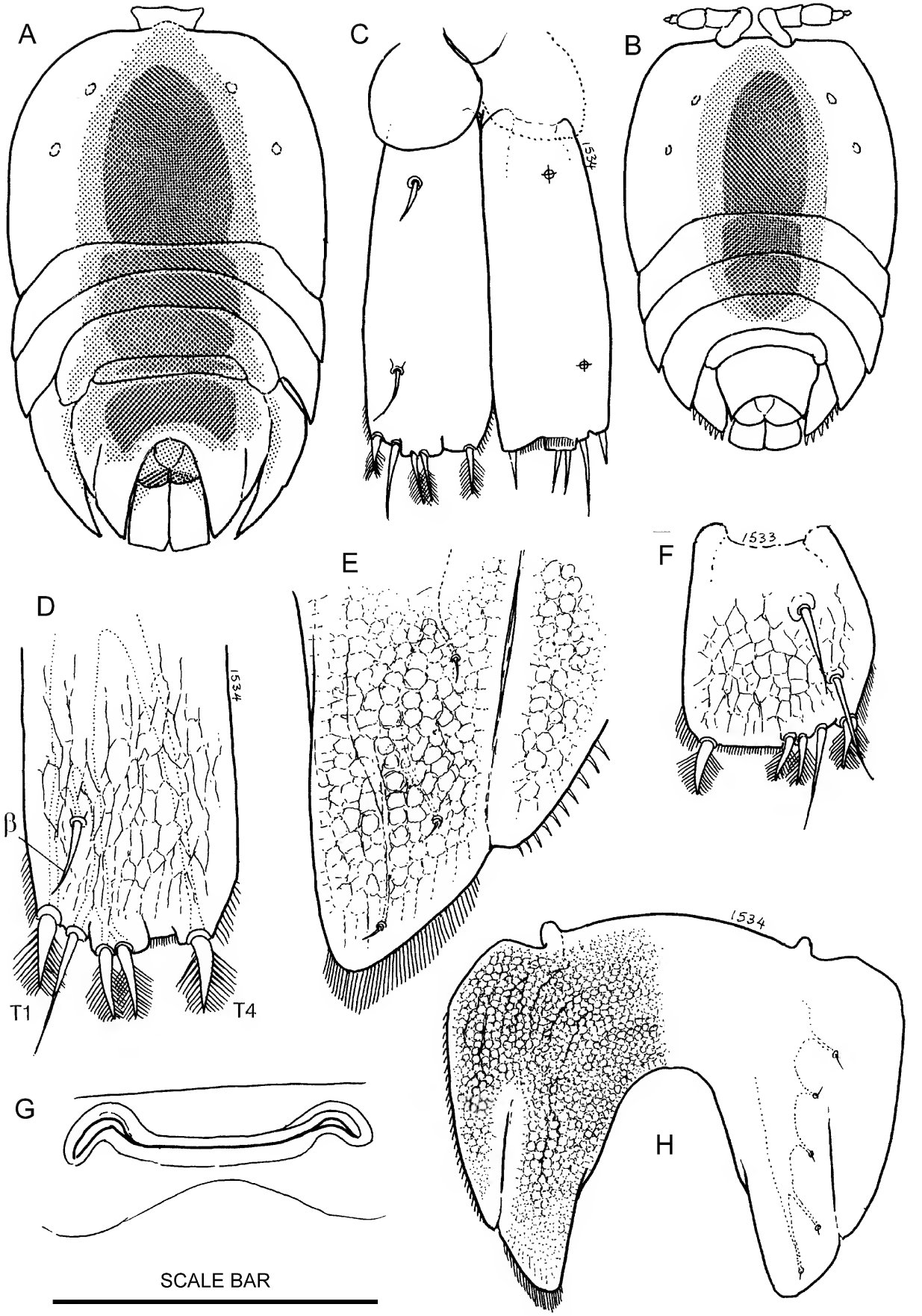

Figure 9. *Porcellidium fimbriatum* Claus, 1863. Female: *(A)* adult showing colour pattern; *(C)* caudal rami (left dorsal, right ventral); *(D)* detail of caudal ramus; *(E, H)* genital double-somite, detail of posterior lobe; *(G)* genital opening. Male: *(B)* adult; *(F)* caudal ramus. Drawings of specimens from Scotland. Scale bar: A, B = 0.45 mm. C = 0.13 mm. D, E, F, G = 0.08 mm. H = 0.23 mm.

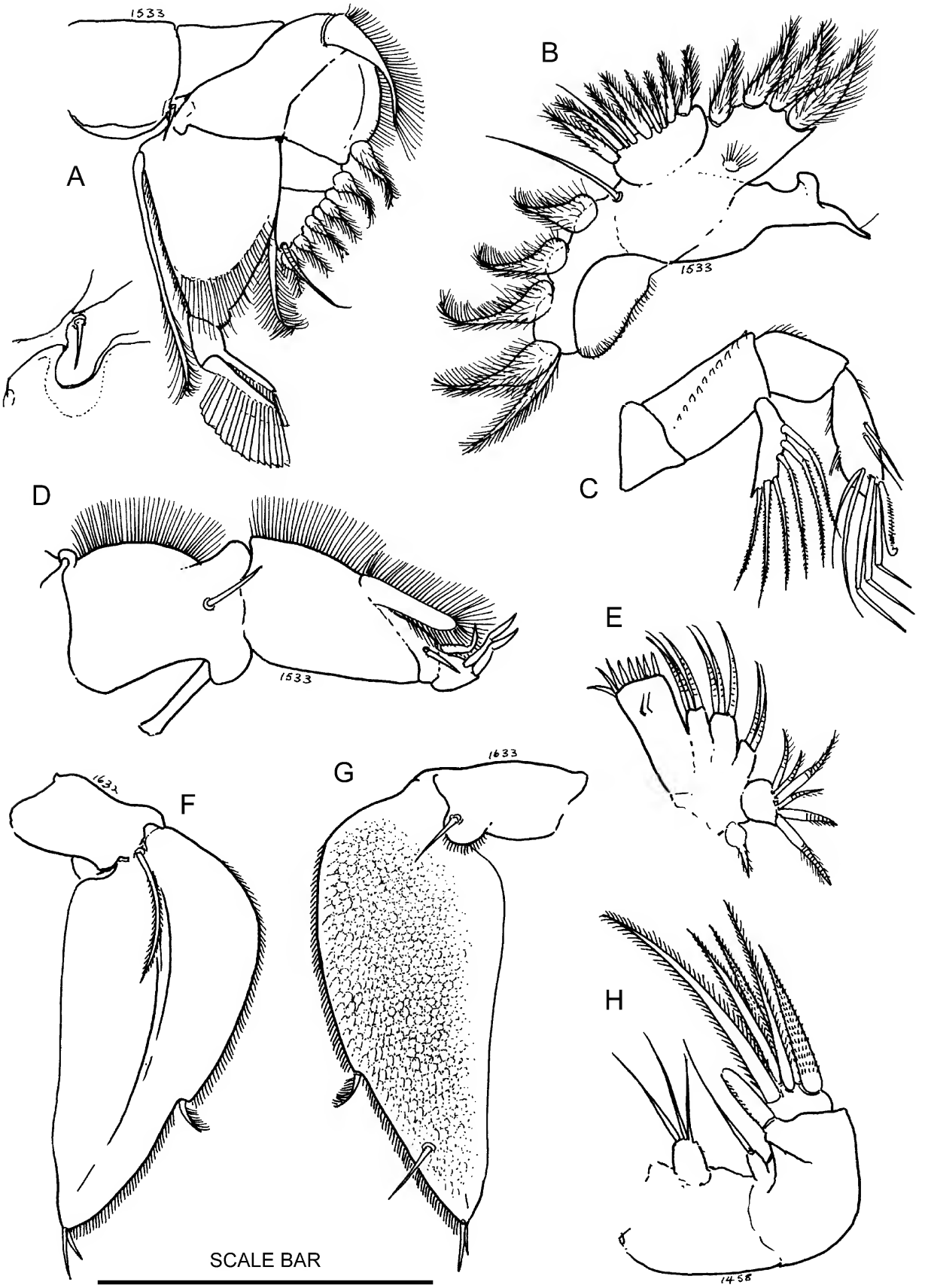

Figure 10. *Porcellidium fimbriatum* Claus, 1863. Female: *(A)* P1 inset showing seta on coxa; *(B)* mandible; *(C)* antenna; *(D)* maxilliped; *(E)* maxillule; *(F, G)* P5 (ventral and dorsal); *(H)* maxilla. Scale bar: A, C = 0.13 mm. B = 0.15 mm. D, E, H = 0.08 mm. F, G = 0.18 mm.

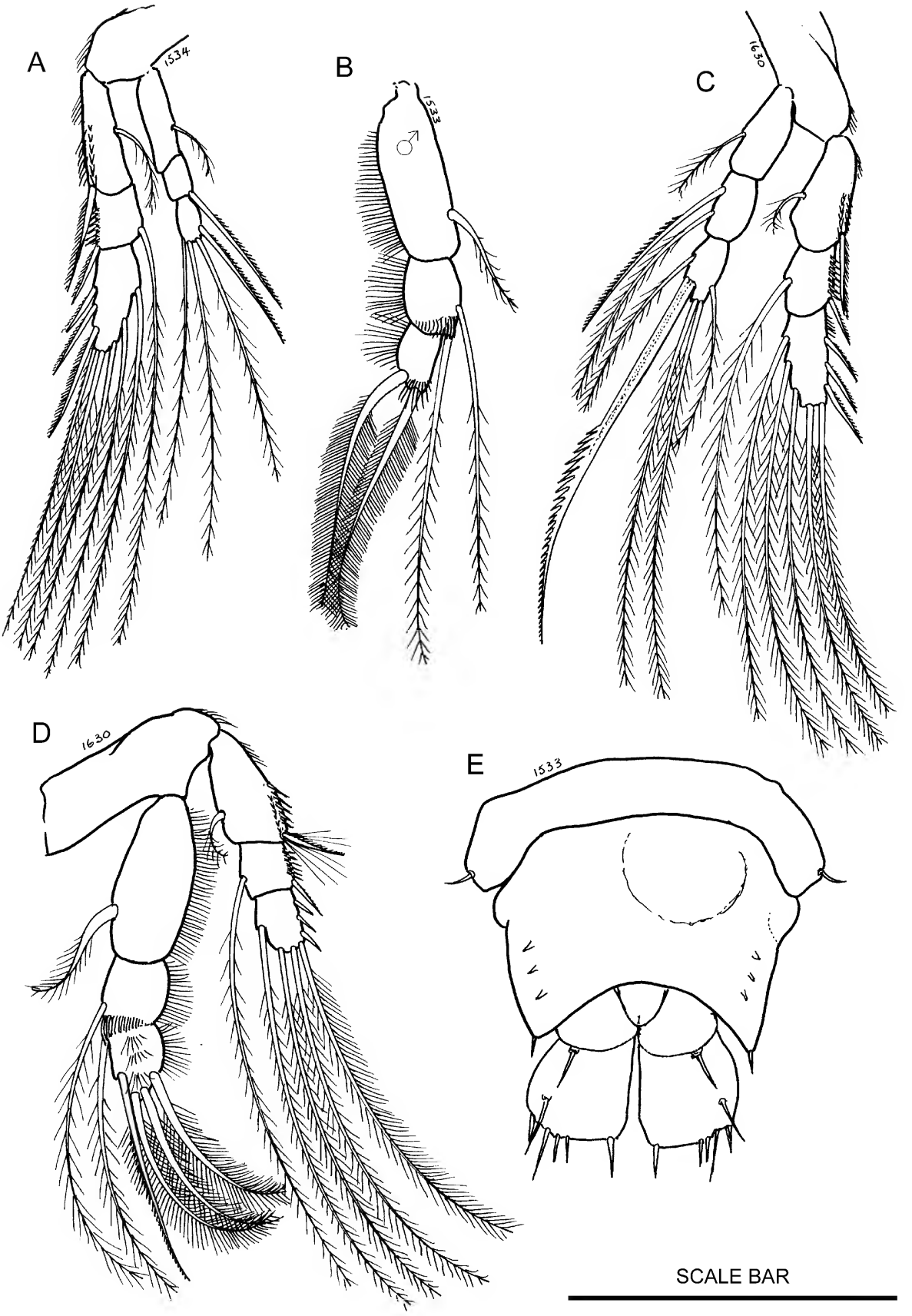

Figure 11. *Porcellidium fimbriatum* Claus, 1863. Female: *(A)* P4; *(C)* P3; *(D)* P2. Male: *(B)* P2 endopod; *(E)* genital somite (dorsal). Scale bar: A, C, D, E = 0.15 mm. B = 0.13 mm.

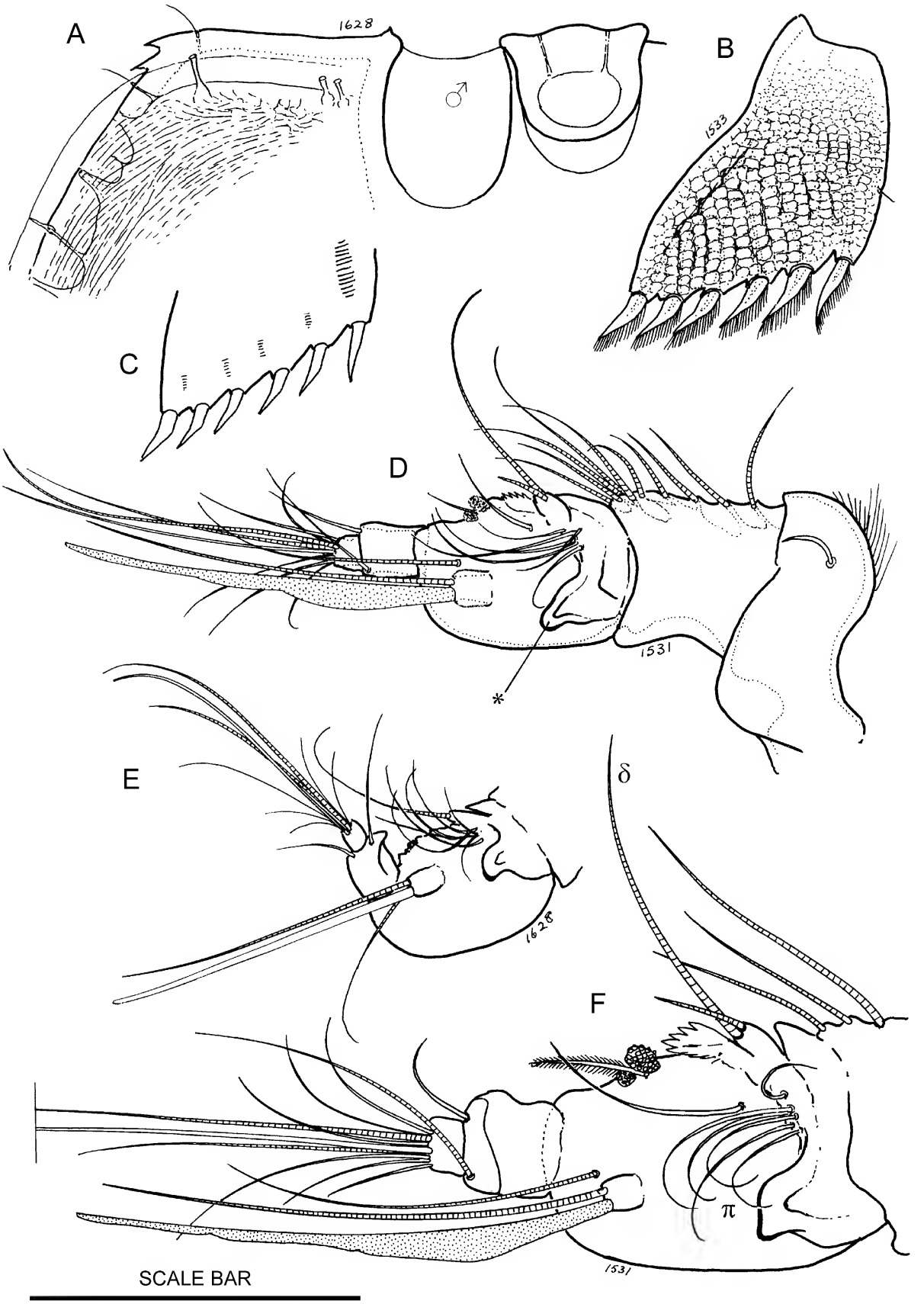

Figure 12. *Porcellidium fimbriatum* Claus, 1863. Male: *(A)* rostrum and shoulder (ventral); *(B, C)* P5 (dorsal, ventral); *(D, E, F)* antennule (* ventral process). Scale bar: A, B, D, E = 0.08 mm. F = 0.06 mm.

Adult males (Fig. 9B; Plate 1E, p. 67). Colouration as for female except that in a few specimens the violet blue colour is absent from posterior region of body. Heavily sclerotized parts of the antennules and antennule sockets are orange on most males. Cephalosome truncated, anterior edge straight (not convex in mid-line), shoulders rounded. Rostrum not wrinkled ventrally, ventral surface of cephalosome with fine wrinkles (Fig. 12A). Dorsal surface with pits as for female. Genital somite with dorsal pits, lateral row of three dorsal sensilla on each side (Fig. 11E). Caudal rami slightly longer than wide (l/w = 1.1), dorsal surface with reticulate markings, medial edge straight, lateral edge convex (Fig. 9F). Beta seta ⅔ down ramus, terminal setae conspicuously pinnate, space between T3 and T4 wider than in female (almost ½ width of ramus) with fringe of fine setules. Antennule (Figs 12D, F) with first seta on segment 2 not longer than 1.5 times length of second seta, segment 3 with short blade-like ventral process, segment 4 with three coupling denticles (proximal with serrated edge, middle and distal denticles small with botryoidal surface, no denticulate pad), dactylus very short, cylindrical (< ⅓ length of segments 3+4), distinctly two segmented, without pronounced terminal hook. P2 endopod with two plumose terminal setae (Fig. 11B), Setae on segments 2 and 3 of P4 endopod all plumose. P5 exopod with dorsal pits (Fig. 12B), ventral setules at base of each terminal seta (Fig. 12C), apical angle of P5 50°.

Remarks. Claus did not explain why he called this species *fimbriatum*, but he must have been impressed by the marked difference between the narrow pointed caudal rami of his *Porcellidium tenuicauda* and the posterior border fringed with bristles of his new 1863 species, (L. *fimbriatum* = separated into shreds or filaments, fringed). Claus redescribed the species in 1889 showing several species specific characters that allowed animals from Scotland to be identified as *Porcellidium fimbriatum*. The species is commonly found with *P.viride* on *Laminaria* in samples from Scotland.

Collection data. *Porcellidium fimbriatum* has been collected from the following algae. *Laminaria* sp., Plymouth, Devonshire, 1970. *Alaria esculenta* and *Gigartina stellata* at Skokholm Island, Pembrokeshire, 1970. *Hymanthalia elongata* at Great Castle Rocks, Dale, Pembrokeshire, Wales, V. A. Harris 1970, 1974. *Chondrus crispus* at Clachan, Seil Sound, Oban Scotland ES2.9/74, 18 ♀♀, 25 ♂♂ and ES18b.11/74, 38 ♀♀, 5 ♂♂ + 13 ♂♂ coupled to juveniles; *C. crispus* and *G. stellata* ES18a.11.74, 72 ♀♀, 28 ♂♂; *Lithothamnion* encrusted stones and boulders ES14.9/74, 3 ♀♀, 1 ♂; *Laminaria saccharina* ES17.9/74, 7 ♀♀, 1 ♂; *C. crispus* and *L. saccharina* ES20.9/97, 76 ♀♀, 16 ♂♂ + 11 ♂♂ coupled with juveniles; *Laminaria digitata* ES19.9/97, 5 ♀♀, 1 ♂, V. A. Harris 1970, 1974, 1987, 1997.

Porcellidium roscoffensis (Bocquet) comb. nov.

Figs 13–16

Porcellidium lecanoides var. *roscoffensis* Bocquet, 1948: 250, fig. IX.
P. lecanoides.—Huys, *et al*. (1996): 308; Wells (2007): 79.
P. viride.—Bodin (1997):64.

Material examined. Specimens collected from mixed seaweeds, Castle Head, Dale, Pembrokeshire, Wales (3 ♀♀, 2 ♂♂) (51°42'N 50°10'W), V. A. Harris, 1970, 1974. Three slide-mounted dissections deposited in NHM, London.

The following account is based on Bocquet's (1948) descriptions of the caudal ramus and genital double-somite of *P. lecanoides* var. *roscoffensis*.

Diagnosis. Male antennule with knob or peg-like ventral process on segment 3, large proximal pad of fine denticles on segment 4, distal denticle with fine comb-like edge, dactylus not broad, concave on one side, hooked terminally, segment 6 inconspicuous, fused to segment 5; ventral surface of male rostrum with U-shaped ridges or wrinkles; indentation (without border setules) marks boundary between anterior and posterior lobes of female genital double-somite, posterior lobe with two sensilla at edge; dorsal surface of male genital somite with five sensilla on each side; dorsal surface of female caudal ramus with pits, β seta close to γ seta.

Biometric data. *Females* (N = 1): body length (L_{urs}) 0.85 mm; cephalosome width (W) 0.60 mm; rostrum width (R) 0.15 mm; genital double-somite width 0.39 mm, length 0.28 mm; caudal ramus length 0.12 mm, width 0.05 mm.

Ratios: L_{urs}/W 1.42; W/R 4.0; genital double-somite width 65% of cephalosome width, w/l 1.4; caudal ramus 14% of L_{urs}, l/w 2.4, Hicks' index for β seta 16%.

Males (N = 1): body length L_{urs} 0.70 mm; body width 0.51 mm.

Ratios: L_{urs}/W 1.4; caudal ramus l/w 0.8; antennule 46% of cephalosome width, segments 3+4 40%, and dactylus 32% of antennule length.

Description. *Adult females* (Fig. 13A): colour (see under *Remarks*). Anterior of cephalosome broadly rounded, rostrum prominent. Dorsal surface ornamented with circular pits 3 µm diameter, no obvious ridges but numerous pit and collared sensilla present on cephalosome, metasome and genital double-somite (see Fig. 13D). Ventral surface of cephalosome smooth, but ventral surface of rostrum has transverse ridges or wrinkles. Hyaline border without striations, 12 µm wide. Labrum without ridge plates or setules. Genital double-somite (Fig. 13D) broad, semicircular in outline, slight lateral notch without setules at that point, two small sensilla at edge of posterior lobe (Fig. 13E), posterior arch deep, encloses most of the caudal rami. Genital opening (Fig. 13F). Caudal ramus (Fig. 13C) rectangular, dorsal surface ornamented with small pits, medial edge straight, medial corner slightly bevelled, lateral edge slightly convex. Terminal setae pinnate, T1 and γ setae recessed at lateral corner, β seta close to γ and posterior edge of ramus, T2 and T3 very close, T4 at medial corner, gap between T3 and T4 less than ½ width of ramus, fringed with fine setules. No finely plumulose setae on segment 2 of antennule, first seta on segment 2 less than 1½ times length of setae 2 or 3. Structure and setation of mouthparts and ambulatory limbs

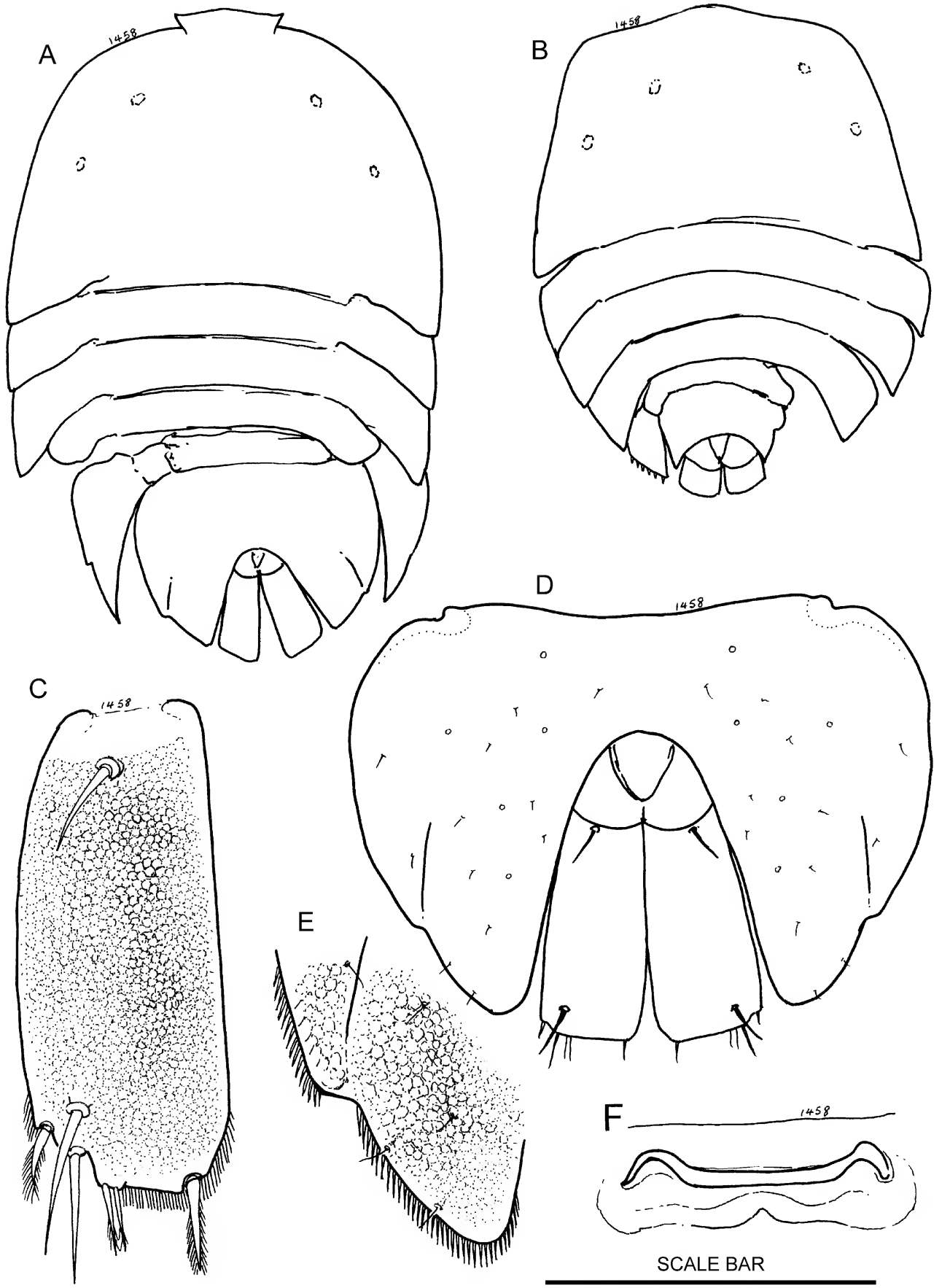

Figure 13. *Porcellidium roscoffensis* (Bocquet, 1948) comb. nov. Female: *(A)* adult; *(C)* caudal ramus; *(D, E)* genital double-somite (*E*, posterior lobe detail); *(F)* genital opening. Male: *(B)* adult. Drawings of specimens from Pembrokeshire. Scale bar: A = 0.48 mm. C, F = 0.08 mm. D = 0.23 mm.

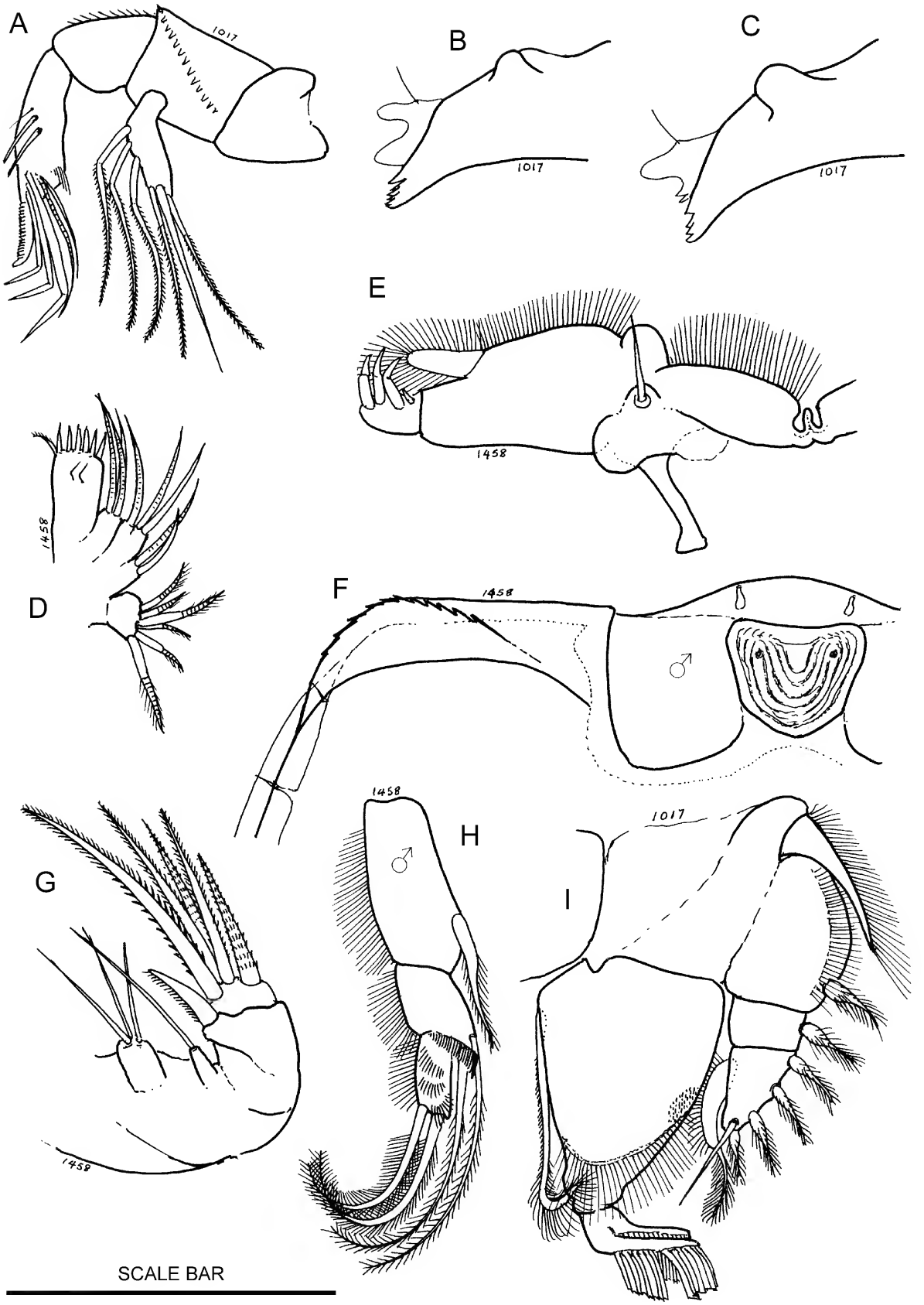

Figure 14. *Porcellidium roscoffensis* (Bocquet, 1948) comb. nov. Female: *(A)* antenna; *(B, C)* molar process of mandible; *(D)* maxillule (exopod seta missing); *(E)* maxilliped; *(G)* maxilla. Male: *(F)* rostrum and shoulder (ventral); *(H)* P2 endopod; *(I)* P1. Scale bar: A, F = 0.13 mm. B, C, D, E, G = 0.08 mm. H, I = 0.15 mm.

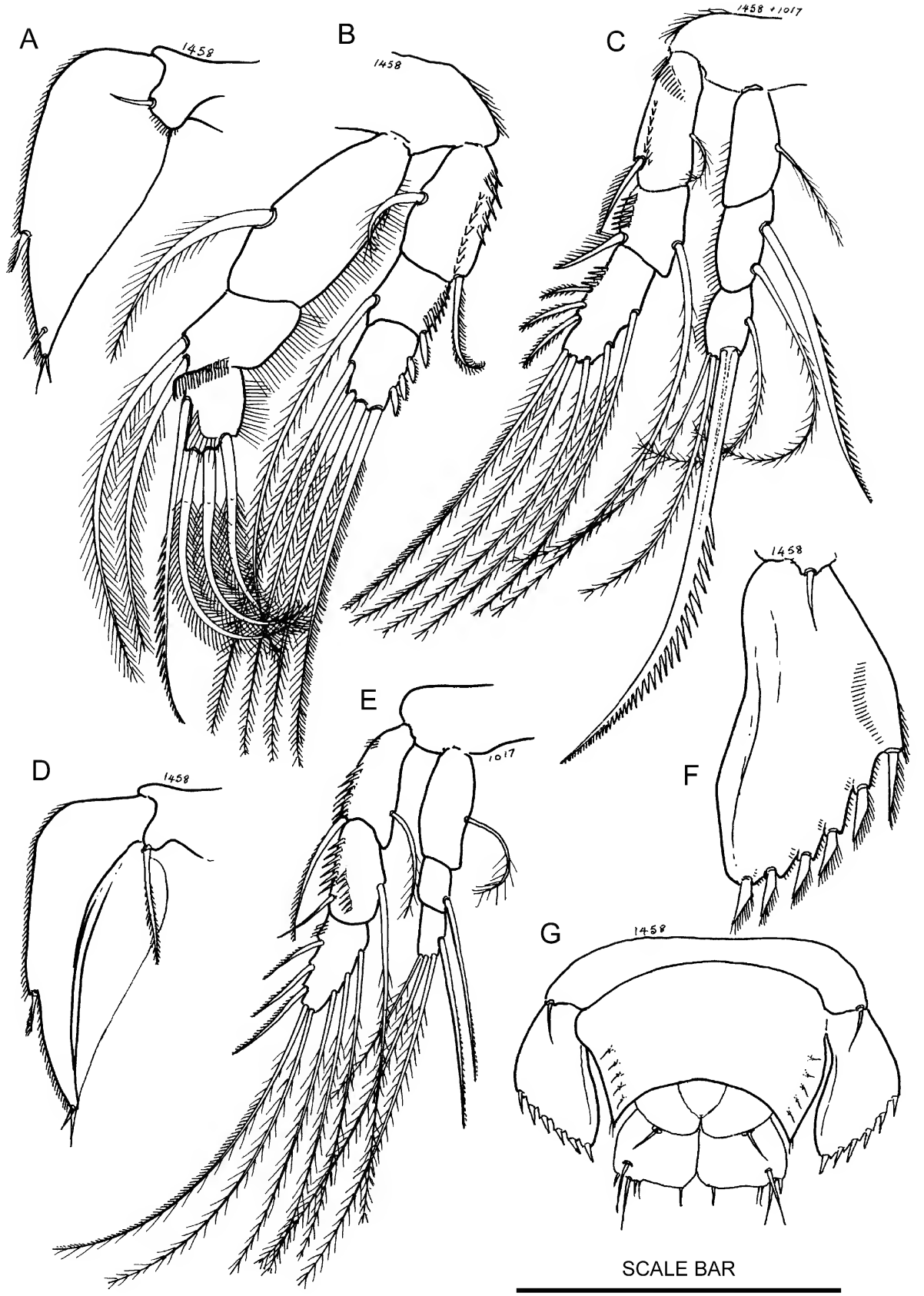

Figure 15. *Porcellidium roscoffensis* (Bocquet, 1948) comb. nov. Female: *(A, D)* P5 (dorsal, ventral); *(B)* P2; *(C)* P3; *(E)* P4. Male: *(F)* P5 (ventral); *(G)* genital somite (dorsal). Scale bar: A, D, G = 0.23 mm. B, C, E = 0.15 mm. F = 0.08 mm.

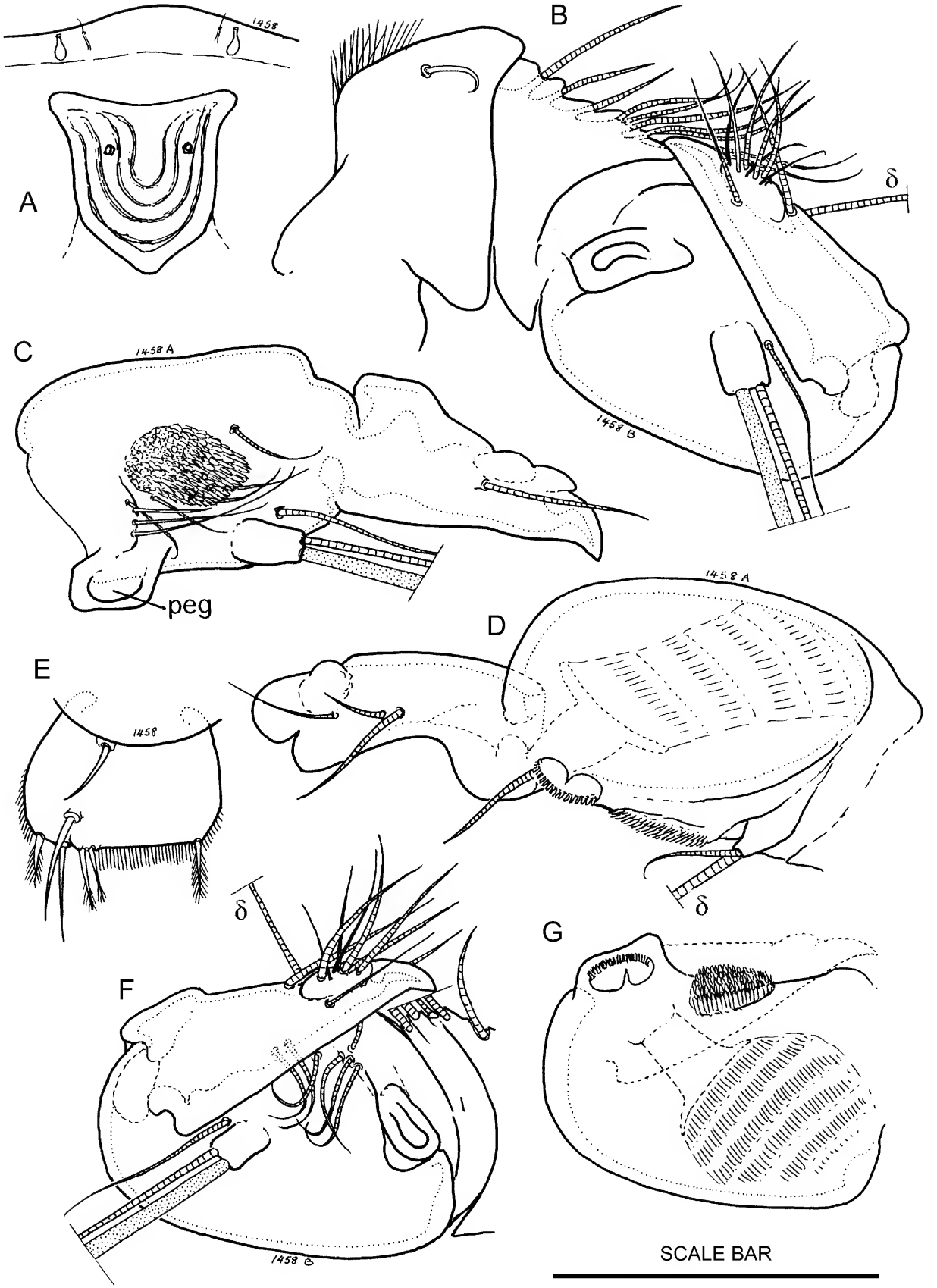

Figure 16. *Porcellidium roscoffensis* (Bocquet, 1948) comb. nov. Male: *(A)* rostrum (ventral); *(B)* antennule; *(C, D, F, G)* details of antennule dactylus and coupling denticles; *(E)* caudal ramus. Scale bar: A–G = 0.08 mm.

typical of family. Antenna (Fig. 14A) with row of triangular setules on basis, three lateral setae on endopod segment 2, end part of geniculate setae plain, terminal claw comb-like about ⅓ length of endopod segment 2. Tips of molar process on mandible (Fig. 14B, C), maxillule (Fig. 11D, exopod not shown), maxilla (Fig. 14G) and maxilliped (Fig. 14E) as described for *Porcellidium viride*. Triangular first segment of P1 endopod narrow (l/w = 1.3), very small peg field at lateral corner of fimbriate crescent (Fig. 14I). Serrate spinous seta on segment 3 of P2 endopod almost as long as endopod (Fig. 15B). Serrate spinous seta on P3 endopod segment 2 (Fig. 15C) as long as endopod, large serrate spinous seta on segment 3 longer than endopod (1.45:1). Seta on P4 endopod segment 2 and internal seta on segment 3 spinous, very finely serrulate (Fig. 15E). Internal seta on baseoendopod of P5 ⅓ length of exopod, exopod lanceolate, dorsal surface with small pits, one subterminal and two apical setae present (Fig. 15A, D). Number of eggs not known, none of the females is ovigerous.

Adult males (Fig. 13B). Cephalosome truncated with rounded shoulders, anterior edge folded ventrally (Fig. 14F). Hyaline border and dorsal ornamentation as described for female. Ventral surface of cephalosome not wrinkled, but ventral surface of rostrum with U-shaped ridges or wrinkles (Figs 14F, 16A). Genital somite with dorsal pits and row of five sensilla on either side (Fig. 15G). Caudal ramus subquadrate (l/w = 0.8), lateral edge convex, medial edge straight, ends in slight bevel with T4 at corner, posterior border straight, T1 and γ setae not recessed, β seta subterminal, fringe of fine border setules between T3 and T4 (Fig. 16E). Antennule (Fig. 16B). No finely plumulose setae on segment 2, first seta less than 1.5 times length of second seta, segment 3 with knob or peg-like ventral process, no spine close to δ seta, proximal coupling denticle on segment 4 large finely denticulate pad, distal denticle with fine comb-like edge (Fig. 16B, C, D, F, G), segment 5 of dactylus almost as long as segments 3+4, concave on one side (Fig. 16D), hooked distally (Fig. 16C), segment 6 inconspicuous. P2 endopod terminates in two plumose setae (Fig. 14H). P5 with short row of small setules at base of each terminal seta (Fig. 15F).

Remarks. Bocquet (1948) describes two colour forms of *P. lecanoides* from Roscoff, Brittany, France. The first is uniform golden yellow, the second is golden yellow with narrow dark violet median stripe down back and caudal rami. Because of their colouration, shape of the caudal rami and statistical difference in size, the second form was considered a variety of Claus' *P. lecanoides* and named *P. lecanoides* var. *roscoffensis*. Bocquet did not give a complete description of the new variety, but the specimens collected from Pembrokeshire conform precisely to Bocquet's illustrations of the caudal rami plus genital double-somite and are considered to be the same species. However, *P. lecanoides* is a synonym for *P.viride* and the Pembrokeshire animals do not resemble *P. viride*. It is considered that Bocquet's variety should be raised to specific rank as *Porcellidium roscoffensis* (Bocquet, 1948) comb. nov.

The antennae of the two male specimens used in this description are either closed or in a position where critical observation of the coupling denticles is difficult. What can be seen is illustrated in Fig. 16.

Distribution. Bocquet (1948) records the species as abundant on *Bifurcaria tuberculata* in tidal pools at Roscoff. It is also abundant in the Bay of Morlaix. Bocquet describes their colour as yellow with a band of violet down the back, but the colour of living animals from Pembrokeshire is not known. They were found among *Porcellidium viride* washed from a mixture of seaweeds many years after collection and were colourless.

Genus *Porcelloides* gen. nov.

Type species. *Porcelloides tenuicaudus* (Claus, 1860) comb. nov.

Porcellidium tenuicauda.—Claus, 1860: 6–8.

Diagnosis. Spermatophore of male reniform (kidney-shaped) with recurrent duct (Fig. 17A, 18C) deposited on dorsal side of female P5, firmly attached on its side by adhesive material, remains attached to female long after egg laying has started (semi-permanent), deposition of more than one spermatophore on female common; male antennule without denticle or ventral process on segment 3, segment 4 with three coupling denticles, proximal denticle triangular with serrated edge, medial denticle large denticulate pad, distal denticle variable (brush-pad absent); outline of male and female body ovoid (egg-shape), anterior of male cephalosome not obviously truncated; hyaline border surrounds edge of cephalosome; female caudal ramus trapezoid or rhomboid; six setae on maxillule endopod, maxilliped coxae touch in midline; dorsal setae of female P5 pinnate, no ventral expansion to P5; male P5 trapezoid with one lateral and five terminal setae.

Species composition. *Porcelloides tenuicaudus* (Claus, 1860) comb. nov.; *Porcelloides scutatus* (Claus, 1889) comb. nov.

Distribution. Genus known from Sicily, Mediterranean Sea; Roscoff, France; Scilly Islands; Ireland; Pembrokeshire, Wales; Scotland.

Remarks. The animals named *Porcellidium tenuicauda* by Claus (1860) are excluded from the diagnosis for *Porcellidium* by apomorphic characters not possessed by *P. viride*. They must be moved to a new genus. The name *Porcelloides* (treated as masculine) is proposed for this new genus. Claus (1860) did not say why he chose the diminutive *Porcellidium* for the name of his new animal, but he might have been impressed by the way they conglobate just like *Porcellio* (the sow bug or woodlouse).

Key to the species of *Porcelloides*

1 Female caudal rami excluded from arch of genital double-somite. T3 absent from caudal ramus, γ seta ½ way down bevelled edge of ramus. Hyaline border of cephalosome not striated. Male rostrum keeled. Terminal setae on male P5 short (< ⅓ length of lateral edge of P5). Colour brown. Europe. (Plate 1G, p. 67) ..... *Porcelloides tenuicaudus* (Claus, 1860) comb. nov.

—— Half female caudal rami included in arch of genital double-somite. T3 present on caudal ramus, γ seta at lateral corner of bevelled edge. Hyaline border of cephalosome striated. Male rostrum not keeled. Terminal setae on male P5 long (⅔ length of lateral edge of P5). Dorsal patch of red/brown on cephalosome. Europe. (Plate 1E, p. 67) ..... *Porcelloides scutatus* (Claus, 1860) comb. nov.

Porcelloides tenuicaudus (Claus, 1860) comb. nov.

Figs 17–20

Porcellidium tenuicauda Claus, 1860: 6–8, taf., II, abb., 10–18.

P. tenuicauda.—Brady, 1880: 166; Claus, 1863: 149; Claus, 1889: 32; Norman & Scott, 1906: 182; Pesta, 1935: 374; Bocquet, 1948: 239–242; Lang, 1948: 422; Bartsch, 1987: 139–143; Huys *et al.*, 1996: 307; Bodin, 1997: 65; Walker-Smith, 2001: 656; Wells, 2007: 79.

Porcellidium dentatum.—Claus, 1860.

Porcellidium ovatum.—Haller, 1879; Haller, 1880: 58.

Material examined. Specimens in NHM, London and NMI, Dublin (see Appendix 1 and 2). Living material was collected for dissection and measurement from the sublittoral at Castle Head, Dale, Pembrokeshire, Wales (51°42'N 5°10'W) and Clachan, Shiel Sound, Oban, Scotland (56°19'N 5°35'W), V. A. Harris, 1974, 1987.

Specimens deposited in NHM, London (1 ♂, 4 ♀♀ and three slide mounted dissections).

The following re-description is based on specimens from Clachan identified from Claus (1860, 1863, 1889) and Bocquet's (1948) description of *Porcellidium tenuicauda* and *P. dentatum*.

Diagnosis. Hyaline border plain (no striations); male rostrum with ventral keel (Fig. 20C); female caudal rami excluded from arch of genital double-somite, ramus acutely trapezoid, apical angle 25°, bevelled edge long (4 × length of lateral edge), marginal setules down whole length of medial and bevelled edge, T1 and γ seta half-way down bevelled edge, T3 absent (Fig. 17D); spinous setae on female P4 endopod segments 2 and 3 slender, finely serrulate; falciform ridge of female P5 a smooth curve (compare Fig. 22E), apical seta not pinnate; terminal setae on male P5 short (⅙ length of exopod lateral edge).

Biometric data. Because animals are not as dorsoventrally flattened as other species and tend to conglobate (roll into a ball) when preserved, some distortion takes place when specimens are mounted flat on a slide. This leads to uncertainty in some of the measurements. There is a wide difference in body length measured to posterior of genital double-somite (L_{urs}) and the total length measured to the extremity of the caudal rami (L_{max}). Both measurements are given. Claus (1860) gives female length as 1⅓ mm and Brady (1880) gives 1/23rd inch (1.1 mm). The following measurements were made on specimens from Scotland and Pembrokeshire, Wales.

Females (N = 6): maximum length (L_{max})1.04 mm (range 0.99–1.10 mm), body length (L_{urs}) 0.89 mm (range 0.87–0.92 mm); cephalosome width (W) 0.74 mm (range 0.71–0.80 mm); rostrum width (R) 0.16 mm (range 0.15–0.18 mm); genital double-somite width 0.35 mm, length 0.29 mm; caudal ramus length 0.19 mm, width 0.07 mm; apical angle of ramus 25–30°.

Ratios: L_{max}/W 1.4 (range 1.22–1.42), L_{urs}/W 1.2 (range 1.13–1.24); W/R 4.5; genital double-somite width 45% of cephalosome width, w/l 1.2, length of posterior lobe 15% of lateral border, arch 24% of genital double-somite length; caudal ramus 21% of L_{urs}, w/l 2.7, Hicks' index for α seta 93%, for β seta 81%.

Males (N = 2): maximum length (L_{max}) 1.0, 1,02 mm, body length (L_{urs}) 0.95 mm; cephalosome width (W) 0.80 mm; apical angle of caudal ramus 25°; antennule fully extended 0.22 mm; spermatophore (N = 4 measured on females) 0.29 × 0.08 mm.

Ratios: L_{max}/W 1.27, L_{urs}/W 1.2; male antennule (fully extended) 28% of cephalosome width, segment 2 32%, segment 3+4 34%, dactylus 18% of antennule length; spermatophore 30% of body length L_{urs}.

Description. *Adult females* (Fig. 17A; Plate 1G, p. 67): colour red-brown partly due to orange oil droplets in body, middle of cephalosome darker in some animals. Body oviform (egg-shape) in outline, cephalosome semicircular, wider (relative to body length) than any other species in the family, body not dorsoventrally flattened to the same extent as most other species (height approximately ¼ cephalosome width). Animals can conglobate. Rostrum projects ⅕ of its width. Hyaline border clear (no striations) with eight sensilla in plane of membrane, width 15 µm. Ducts of marginal glands open dorsal to hyaline membrane. Dorsal surface with small pits 4–5 µm in diameter, medial portion of P5 and dorsal surface of caudal rami ornamented with network of ridges (Figs 17D, 19D, 20B). Genital double-somite (Fig. 17B) narrow, ½ cephalosome width, length about ⅕ body length, posterior lobe short (⅙ lateral border), not expanded laterally, bordered with a few filiform setules, posterior arch houses anal somite only, caudal rami completely excluded from arch. Genital aperture simple (Fig. 17C). Caudal ramus trapezoid, elongate, acute pointed, (l/w = 2.6). Seta T4 large

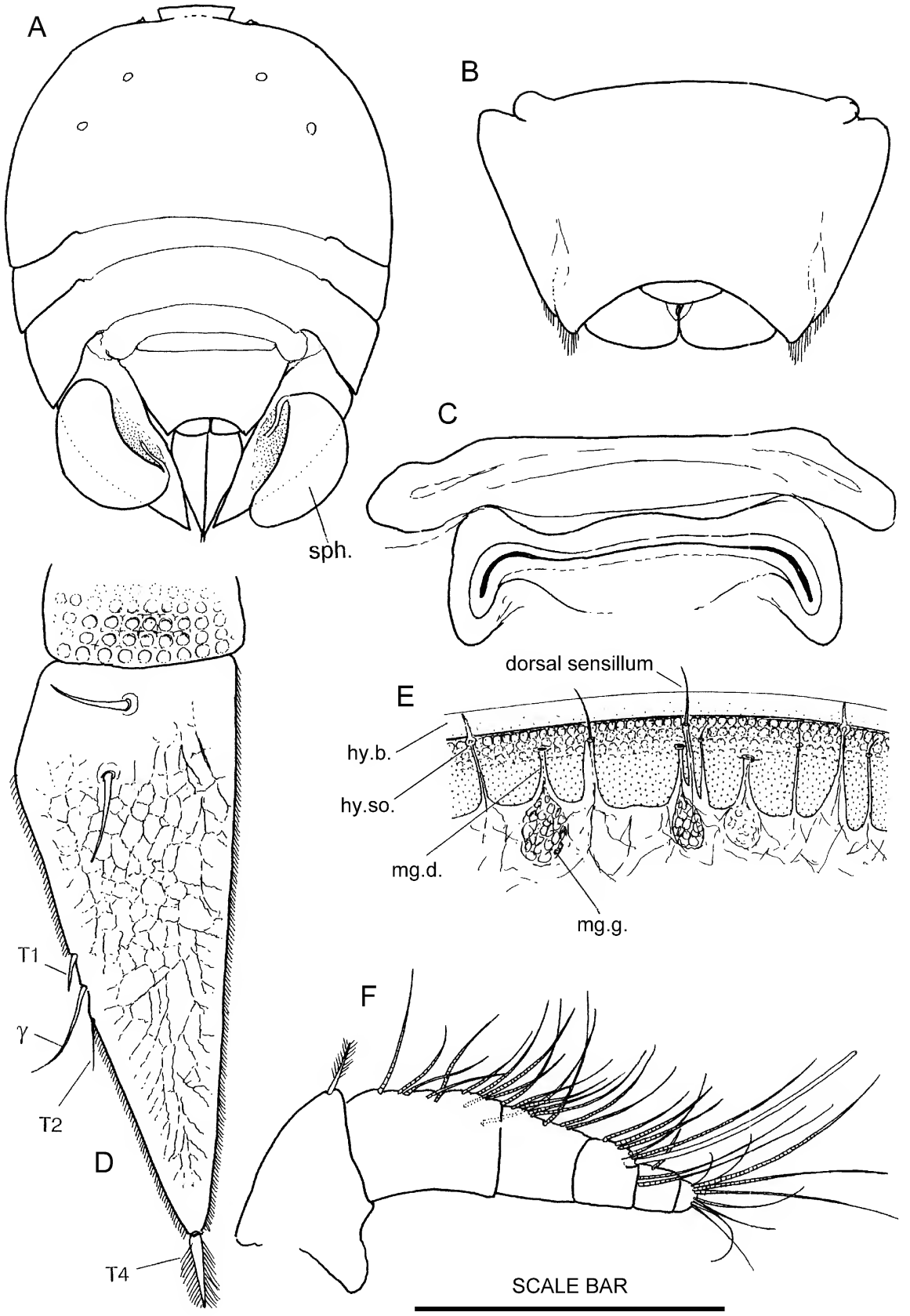

Figure 17. *Porcelloides tenuicaudus* (Claus, 1860) comb. nov. Female: *(A)* adult (carrying two empty spermatophores on dorsal surface of P5s; *(B)* genital double-somite; *(C)* genital opening; *(D)* caudal ramus (dorsal); *(E)* border of cephalosome (*hy.b.* hyaline membrane; *hy.so.* hyaline sense organ; *mg.d.* duct; *mg.g.* marginal gland); *(F)* antennule. Scale bar: A = 0.65 mm. B = 0.25 mm. C, D = 0.1 mm. E = 0.2 mm. F = 0.14 mm.

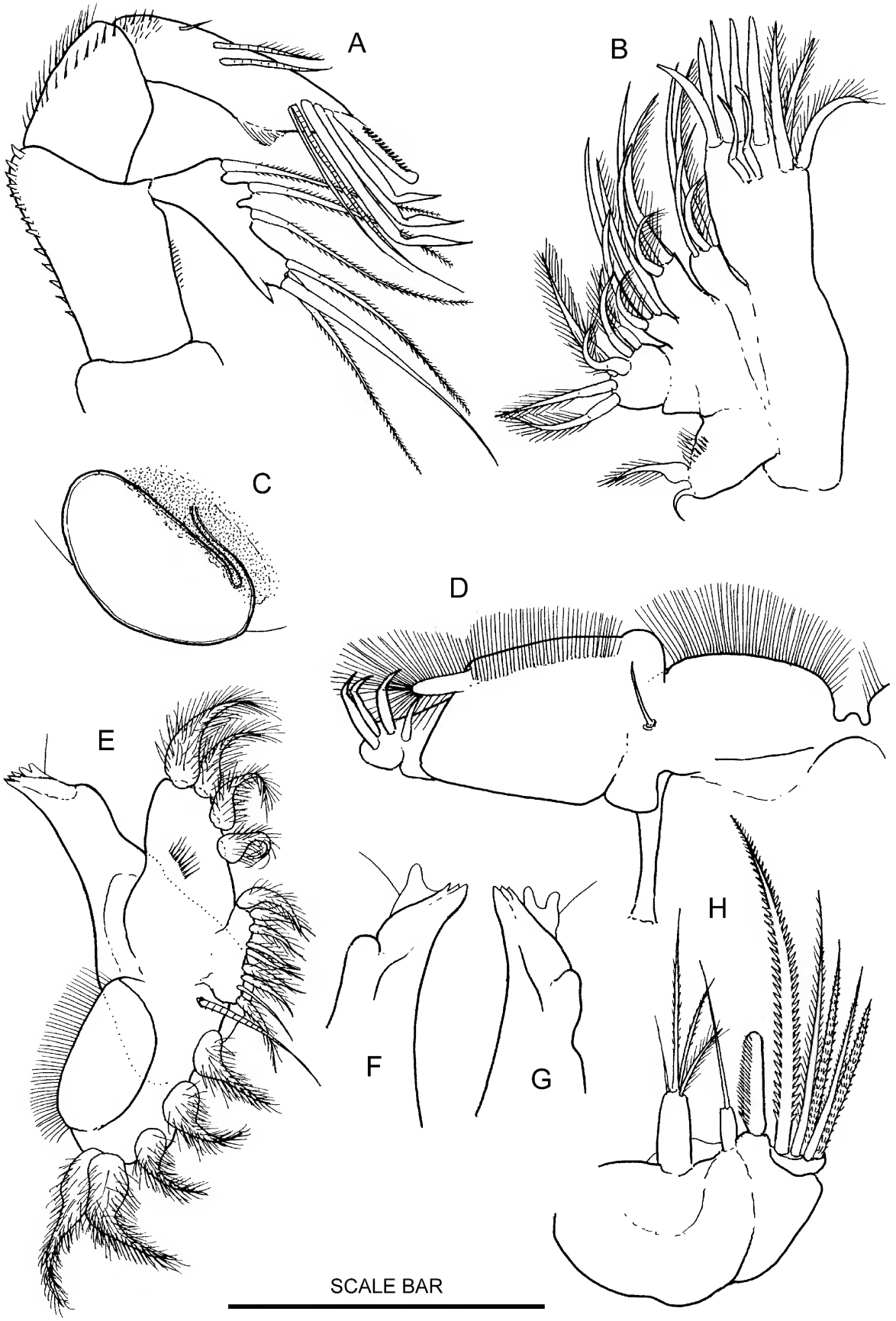

Figure 18. *Porcelloides tenuicaudus* (Claus, 1860) comb. nov. Female: *(A)* antenna; *(B)* maxillule; *(C)* empty spermatophore attached to P5; *(D)* maxilliped; *(E)* mandible; *(F, G)* right and left molar process; *(H)* maxilla. Scale bar: A, D, H = 0.1 mm. B = 0.08 mm. C = 0.4 mm. E = 0.19 mm. F, G = 0.14 mm.

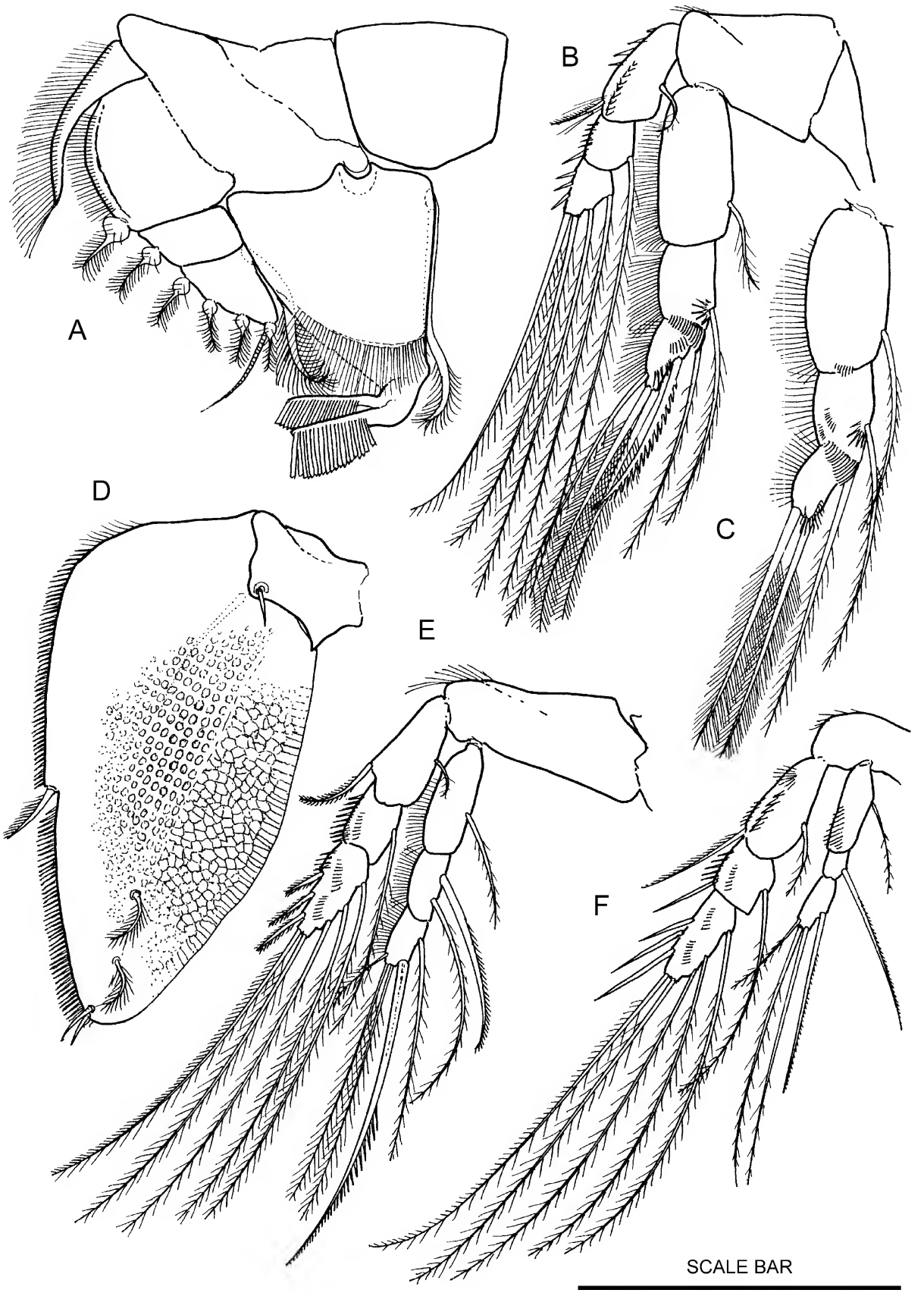

Figure 19. *Porcelloides tenuicaudus* (Claus, 1860) comb. nov. Female: *(A)* P1; *(B)* P2; *(D)* P5 (dorsal); *(E)* P3; *(F)* P4. Male: *(C)* P2 endopod. Scale bar: A = 0.16 mm. B, C, E, F = 0.22 mm. D = 0.25 mm.

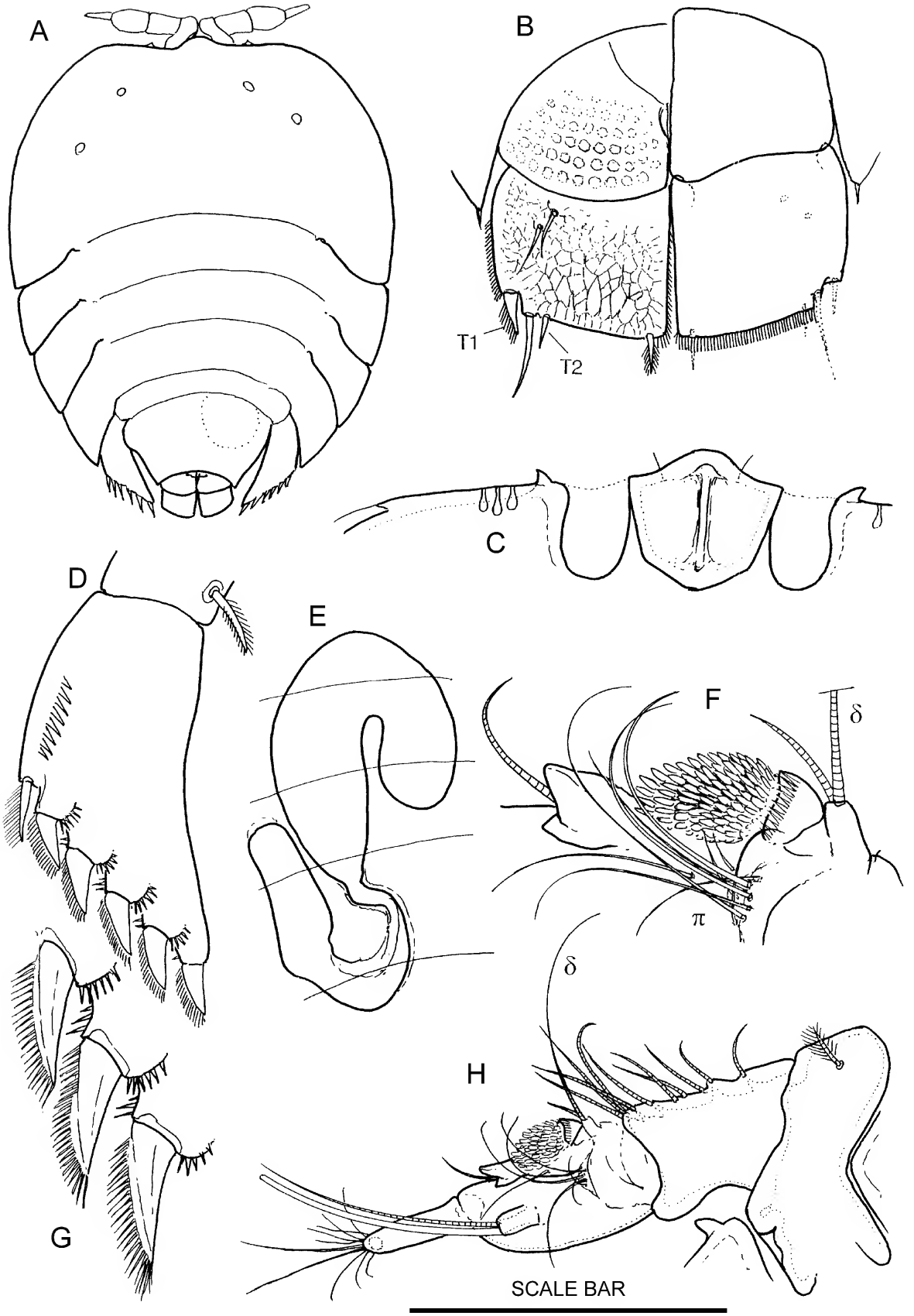

Figure 20. *Porcelloides tenuicaudus* (Claus, 1860) comb. nov. Male: *(A)* adult; *(B)* caudal rami (left dorsal, right ventral); *(C)* rostrum (ventral); *(D, G)* P5 (ventral, detail of terminal setae); *(E)* developing spermatophore; *(F)* coupling denticles on antennule; *(H)* antennule. Scale bar: A = 0.65 mm. B = 0.14 mm. C, D = 0.15 mm. E = 0.3 mm. F = 0.06 mm. G = 0.08 mm. H = 0.12 mm.

pinnate at posterior apex (Fig. 17D), medial edge straight, bordered with fine setules along entire length, lateral edge divergent, without setules, extends as far as level of β seta, bevelled edge 4 × length of medial edge, bordered with fine setules, α and β setae inserted proximally, terminal seta T1 small inserted about ⅓ down bevelled edge, γ and T2 about ½ way down bevelled edge, T3 absent. Antennule, segment 1 seta pinnate (Fig. 17F), no plumulose setae on segment 2. Setation of mouthparts and ambulatory limbs typical of family. Basis and segment 1 of antenna endopod with setules along medial border, exopod with five plumulose setae and one plain spinous seta, segment 2 of endopod with one small and two longer lateral setae (1 pinnate), geniculate setae with distal part plain, claw comb-like (Fig. 18A). Anterior lobe of mandibular palp with small patch of ventral setules (Fig. 18E). Gnathobase of maxillule precoxa (Fig. 18B) with five plain and three pinnate setae plus two lateral geniculate setae, endite on coxa and two endites on basis with four setae each, endopod with six setae, exopod with one plain and one bulbous seta. Proximal endite on syncoxa of maxilla (Fig. 18H) with four setae, distal endite with one seta, spatulate seta on basis with comb-like edge, endopod with three biserrulate and two multi-serrulate setae. Maxilliped coxae touch in midline, basis with fimbriate border and fimbriate process (Fig. 18D). No peg area on P1 endopod, endopod l/w = 1.05, terminal claws of endopod lamellate (Fig. 19A). P2 endopod 1½ times length of exopod (Fig. 19B), external seta on exopod segment 1 short, terminal segment of endopod with strong, serrate spinous seta plus three plumose setae. P3 (Fig. 19E) spinous seta on segment 2 of endopod finely serrulate, shorter than endopod (0.75:1), large spinous seta on terminal segment slender, serrate, longer than endopod (1.4:1). P4 endopod ⅔ length of exopod (Fig. 19F), external seta on segment 1 of exopod as long as segment 1, spinous seta on endopod segment 2 and first (internal) spinous seta on segment 3 both long, thin and finely serrulate. P5 (Fig. 19D) baseoendopod with small plain external and serrulate internal seta, exopod broad, ovate (*w/l = 0.45), bordered along external edge with short setules, dorsal surface with pits except for medial edge which has a reticulate pattern, two large pinnate dorsal setae plus two plain setae at apex. P5s reach to posterior extremity of caudal rami. (* Width of P5 at level of lateral seta).

Adult males (Fig. 20A). Colour, body shape, hyaline border and dorsal pits as for female. Anterior edge of cephalosome rounded, slightly truncated, rostrum with ventral keel, only visible from ventral view, projects as convex bulge in midline (Fig. 20C), lateral angle of antennule socket with conical projection. Caudal ramus short, almost quadrate (Fig. 20B), lateral edge convex with setules down posterior ⅔, medial edge straight with fine setules down length, α and β setae short (¼ width of ramus), T1 pinnate, short, slightly recessed, T2 very short, plain, T3 absent, T4 pinnate, close to medial corner, posterior border with fine setules, dorsal surface of rami with fine reticulate pattern. Antennule short, 28% of cephalosome width with dactylus fully extended, (Fig. 20A, H), segment 1 expanded medially to touch its fellow in front of rostrum, segment 3 with anterior process bearing δ and δ' setae, and π series, segment 4 with proximal triangular coupling denticle, large denticulate pad and bicuspid distal denticle (Fig. 20F), dactylus (segment 5) cylindrical (½ length of segment 3+4), hooked distally, segment 6 small, fused to segment 5. Ambulatory limbs differ from female as follows. Endopod of P2 with two plumose terminal setae (Fig. 19C). P5 exopod trapezoid (Fig. 20D), length of terminal setae < ⅓ of P5 lateral edge, first (lateral) seta narrower than rest of terminal setae, ventral row of six or seven setules at base of each terminal seta (Fig. 20G). Developing spermatophore *S*-shaped (Fig. 20E), reniform (kidney or bean-shaped) with recurrent duct when fully formed and deposited on female P5 (Fig. 18C).

Remarks. Only a few isolated specimens of *Porcelloides tenuicaudus* have been found after extensive sampling on the West coast of Scotland and Pembrokeshire, Wales, which suggests the animal's preferred habitat was not sampled. The typical dorsoventral flattened body of most porcellidiid species is correlated with life in fast flowing or turbulent waters of the littoral zone where the shape of their body enables them to hold on tenaciously to the substratum. When *P. tenuicaudus* is subjected to fast flowing water (i.e., a jet from a pipette) it rolls into a ball and detaches from the substratum (personal observation). This suggests that its normal habitat may be in deeper water away from fast flowing currents. Haller (1879) dredged his *Porcellidium ovatum* (= *Porcelloides tenuicaudus*) from 80–150 metres and Brady dredged it from 10 fathoms near the Scilly Islands.

Distribution. In the present study specimens were collected from the following algae. *Himanthalia elongata* at Castle Bay, Dale, Pembrokeshire (51°42'N 5°10'W), (4 ♀♀), V. A. Harris, 1974. From *Chondrus crispus*, holdfasts of *Laminaria saccharina*, and stones covered with pink *Lithothamnion*, in the sublittoral at Clachan, Shiel Sound, Oban, Scotland (56°19'N 5°35'W), (4 ♀♀, 2 ♂♂), V. A. Harris, 1974, 1987.

In literature (*cf.* Lang, 1948) it is reported from Shetland Islands, Ireland, Scilly Islands, W coast of France and Mediterranean Sea.

Porcelloides scutatus (Claus, 1889) comb. nov.

Figs 21–24

Porcellidium scutatum Claus, 1889: 34, taf., VIII, abb., 9–18.
Porcellidium ovatum.—Lang, 1948: 442; Geddes, 1968: 14; Holmes & O'Conner, 1990: 66; Huys *et al*., 1996: 307, 123; Wells (2007): 79.

Material examined. Spirit material and prepared slides in NMI, Dublin, collected by D. Minchin and J.M.C. Holmes from Loch Hyne (Ine), Co. Cork, Ireland (9°15'W 51°30'N), (see Appendix 2). Living material, used for measurements and the following description, was collected from red alga (?*Gelidium* sp.) Loch Hyne, Co. Cork, Ireland and identified from species specific characters in Claus' 1889 description of *Porcellidium scutatum.*

Specimens of *Porcelloides scutatus* (4 ♀♀, 5 ♂♂ and five dissections mounted on slides) have been deposited at NHM, London, V. A. Harris, 1997.

Diagnosis. Hyaline border appears striated; about ½ female caudal ramus lies in arch of genital double-somite; female caudal ramus trapezoid, apical angle 50°, bevelled edge almost equal in length to lateral edge, T1 and γ setae at lateral corner of bevelled edge, T2 normal, T3 very thin, inconspicuous, no setules along medial edge (Fig. 22H); female P4 with massive serrated spinous setae on segments 2 and 3 of endopod (Fig. 23B); ventral falciform ridge on female P5 undulating (wavy), apical seta pinnate (Fig. 22D,

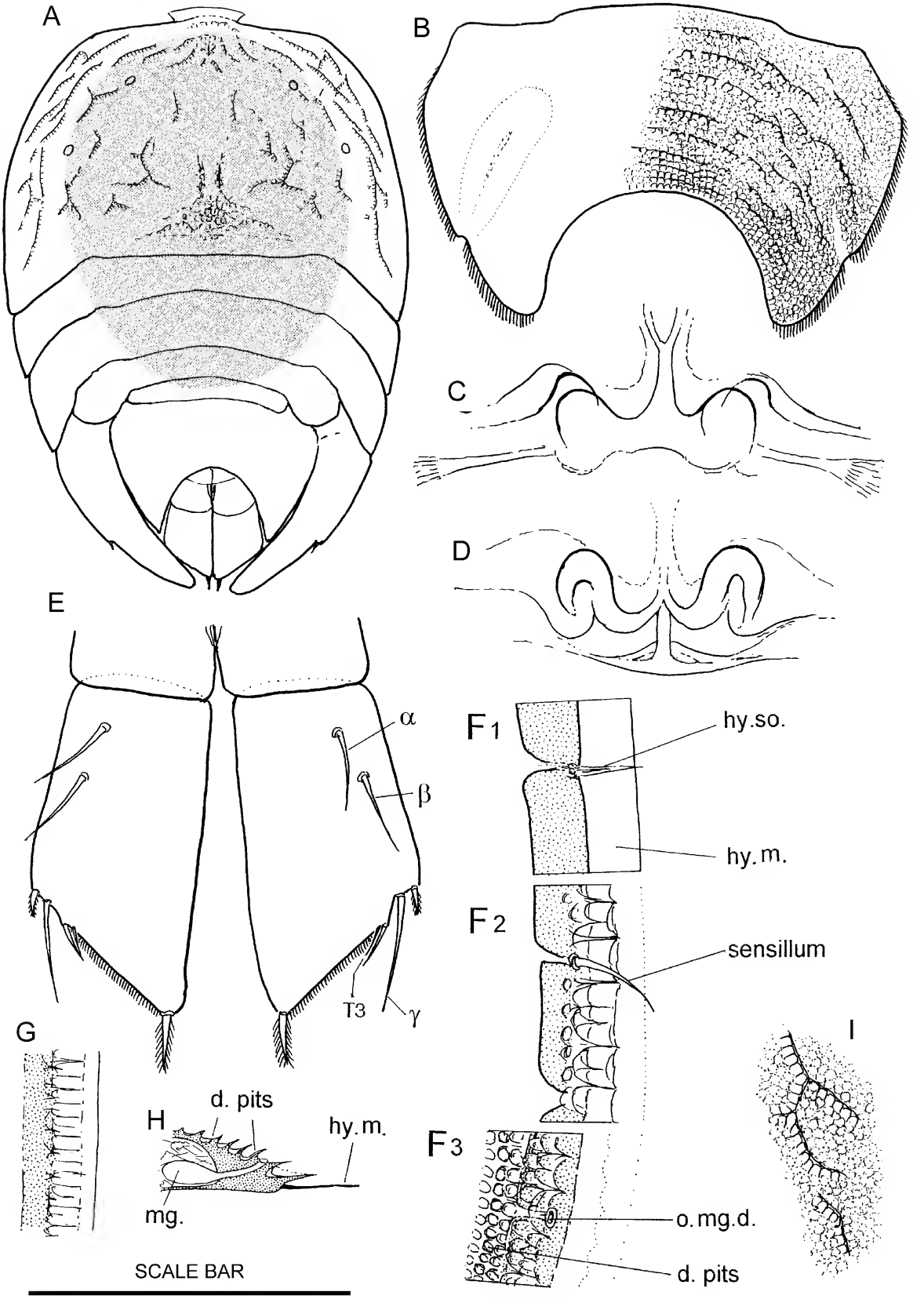

Figure 21. *Porcelloides scutatus* (Claus, 1889) comb. nov. Female: *(A)* adult*; *(B)* genital double-somite; *(C, D)* genital opening, superficial and deep focus; *(E)* caudal rami; *(F)* cephalosome border, F_1 focus in plane of hyaline membrane; F_2 focus above membrane showing cuticular ridges; F_3 dorsal focus showing dorsal pits (*d. pits, hy.m.* hyaline membrane; *hy.so.* hyaline sense organ; *o.mg.d.* opening of marginal gland duct); *(G)* appearance of border showing false striations; *(H)* diagrammatic section through cephalosome border (*mg.* marginal gland); *(I)* dorsal cuticular ridges on cephalosome. *Drawing of specimen from Ireland. Scale bar: A = 0.45 mm. B = 0.23 mm. C, D = 0.1 mm. E = 0.14 mm. F = 0.07 mm.

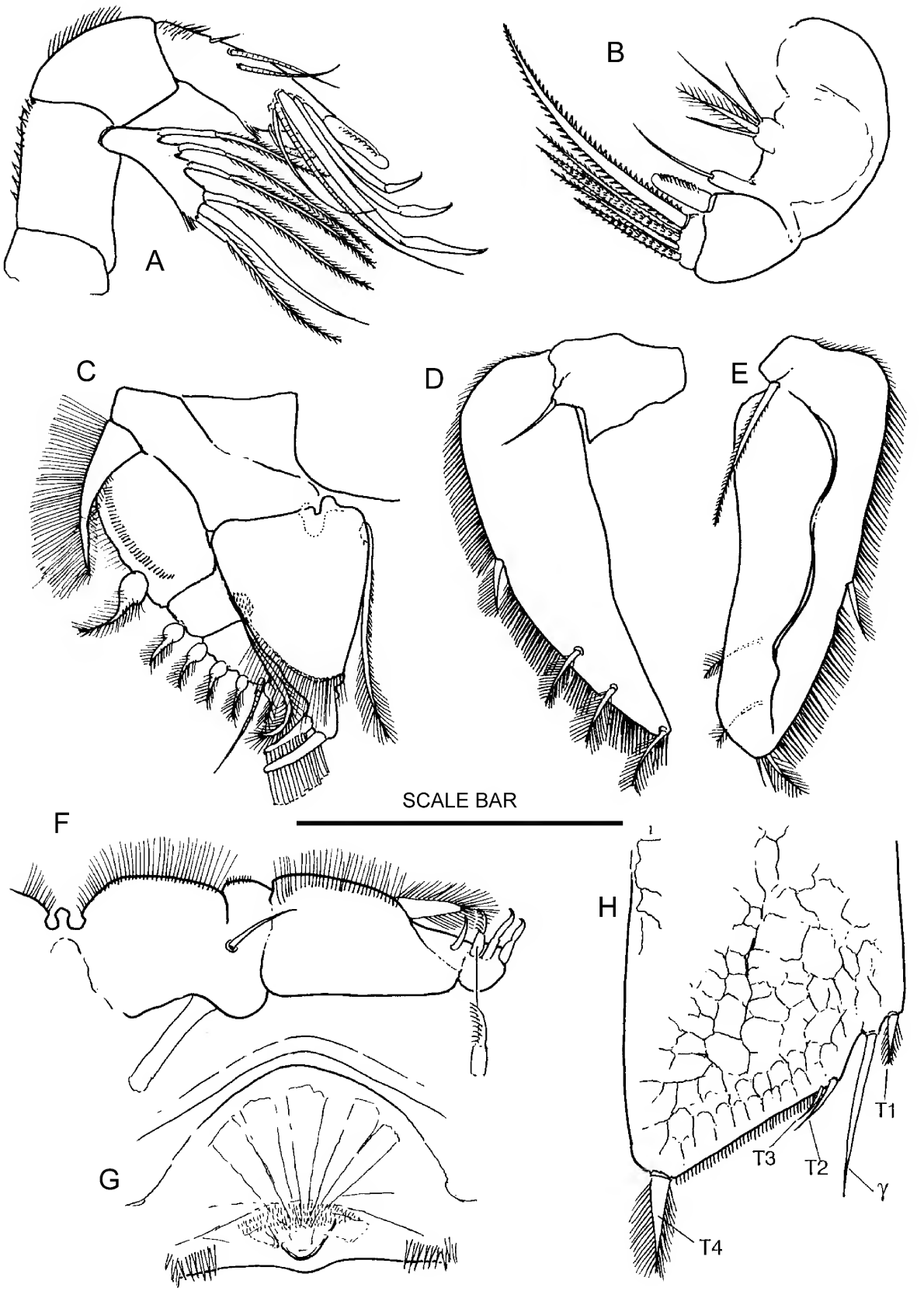

Figure 22. *Porcelloides scutatus* (Claus, 1889) comb. nov. Female: *(A)* antenna; *(B)* maxilla; *(C)* P1; *(D, E)* P5 (dorsal and ventral, showing pinnate dorsal setae and undulating ventral falciform ridge); *(F)* maxilliped; *(G)* labrum; *(H)* caudal ramus (detail). Scale bar: A, B, F, G = 0.1 mm. C = 0.19 mm. D, E = 0.25 mm. H = 0.08 mm.

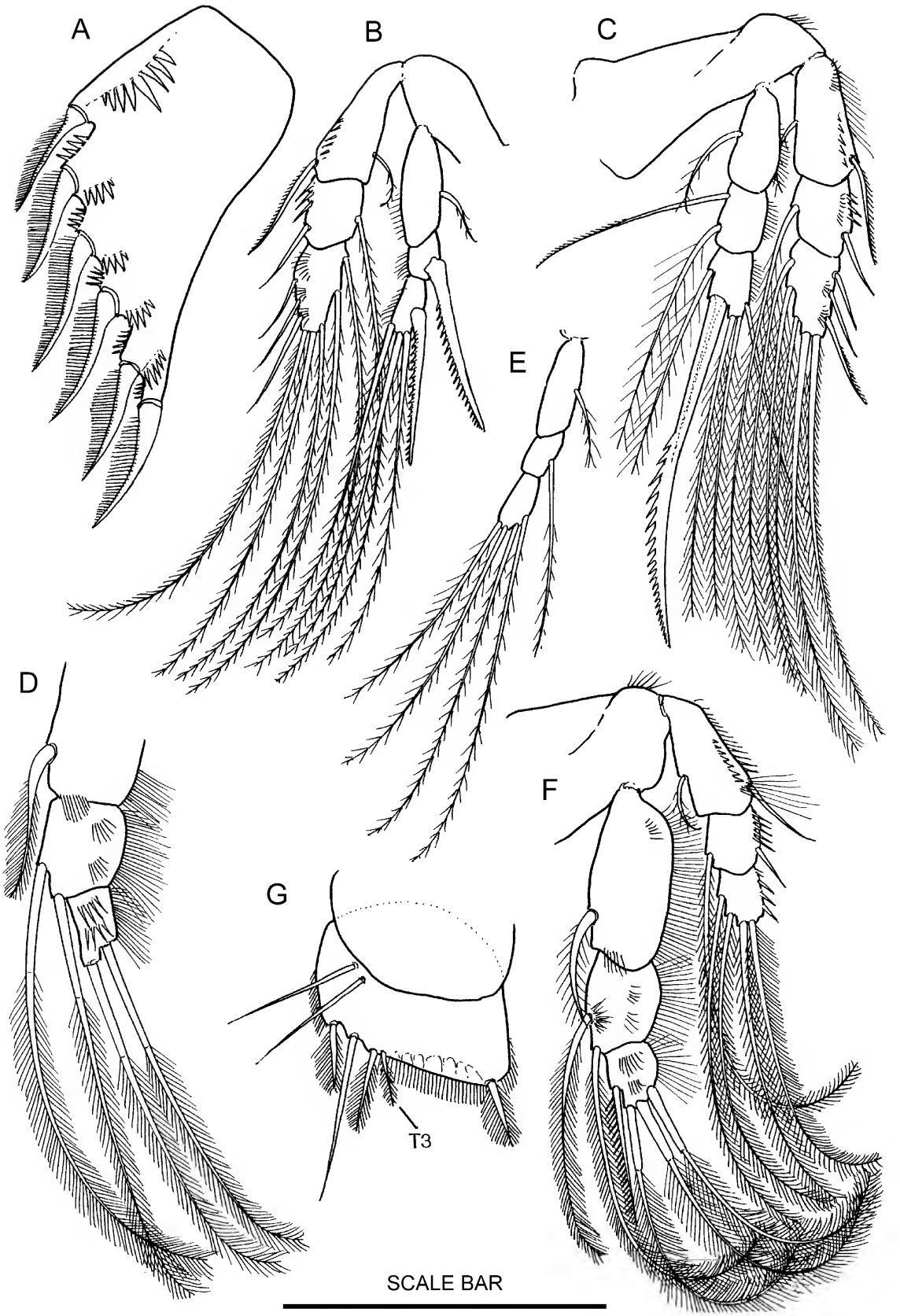

Figure 23. *Porcelloides scutatus* (Claus, 1889) comb. nov. Male: *(A)* P5 (ventral); *(D)* P2 endopod; *(E)* P4 endopod; *(G)* caudal ramus. Female: *(B)* P4; *(C)* P3; *(F)* P2. Drawing of specimen from Ireland. Scale bar: A, G = 0.1 mm. B, C, E, F = 0.15 mm. D = 0.14 mm.

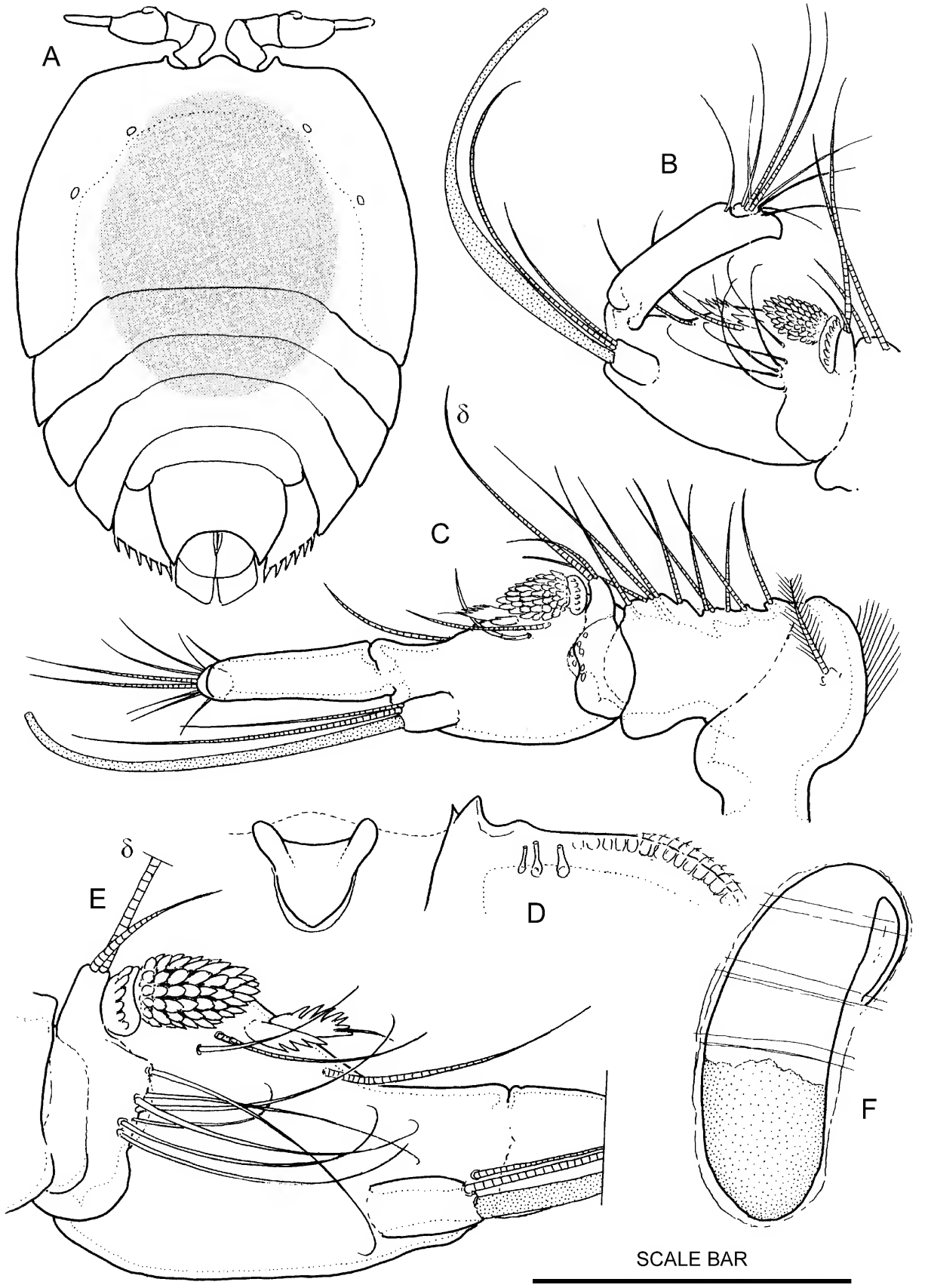

Figure 24. *Porcelloides scutatus* (Claus, 1860) comb. nov. Male: *(A)* adult; *(B, C)* antennule (ventral, π setae omitted in *C*); *(D)* rostrum and anterior border of cephalosome (ventral); *(E)* detail of coupling denticles on antennule; *(F)* spermatophore. Scale bar: A = 0.45 mm. B, C = 0.11 mm. D = 0.15 mm. E = 0.06 mm. F = 0.23 mm.

E); terminal setae on male P5 exopod long (>½ length of lateral edge).

Biometric data. *Females* (N = 11): maximum length (L_{max}) 0.84 mm, body length (L_{urs}) 0.78 mm (range 0.74–0.83 mm) [female body length from literature 0.75–0.80 mm, Claus (1889)]; cephalosome width (W) 0.56 mm; rostrum width (R) 0.11 mm; genital double-somite width 0.38 mm, length 24.5 mm; caudal ramus length 0.135 mm, width 0.075 mm; apical angle of ramus 50°.

Ratios: L_{max}/W 1.52, L_{urs}/W 1.4; W/R 5.1; genital double-somite width 68% of cephalosome width, w/l 1.54, length of posterior lobe 30% of lateral border, arch 40% of genital double-somite length; caudal ramus 17% of L_{urs}, l/w 1.8, Hicks' index for α seta 88%, for β seta 72%.

Males (N = 8): maximum length (L_{max}) 0.78 mm, body length (L_{urs}) 0.70 mm; cephalosome width (W) 0.53 mm; apical angle of caudal ramus 70°; antennule fully extended 0.23 mm; spermatophore 0.25 × 0.087 mm (measured on female P5).

Ratios: L_{max}/W 1.47, L_{urs}/W 1.3; antennule 43% of cephalosome width, segment 2 26%, segment 3+4 39%, dactylus 28% of antennule length; spermatophore 36% of body length (L_{urs}).

Description. *Adult females* (Fig. 21A; Plate 1F, p. 67): central area of cephalosome and metasome reddish-brown, rest of body colourless. Body ovoid in outline, dorsoventrally depressed, anterior slightly truncated, rostrum prominent with hyaline border, not obscured by anterior bulge of cephalosome. Animals do not conglobate. Dorsal pits conspicuous, 3–5 µm, area round pits slightly thickened to form cuticular network (Fig. 21I), very few dorsal sensilla. Hyaline border appears to have striations perpendicular to edge (Fig. 21G). Striations due to network of ridges expanding out above hyaline border (Fig. 21F_2, H), hyaline border itself is without striations (Fig. 21F_1). Cuticular striations 7–9 µm wide, hyaline border 11–13 µm wide (Fig. 21F_2). Labrum with central patch of very short setules plus group of about eight setules on either side of posterior edge (Fig. 22G). Sternum of metasome segment 4 with fimbriate setules along posterior border. Genital double-somite short, broad (Fig. 21B), small lateral notch and area devoid of pits or setules marks boundary between anterior and posterior lobes, posterior lobe short (⅓ of lateral edge), both lobes fringed with fine setules. Posterior arch almost half length of genital double-somite, accommodates anal segment and ⅔ of caudal rami (as far as lateral corner of the bevelled edge). Genital opening (Fig. 21C, D). Caudal ramus trapezoid (Fig. 21E), widens slightly posteriorly (maximum width ⅔ down ramus where bevelled edge starts), medial edge without setules, T1 pinnate close to γ at lateral corner of bevelled edge, T2 tends to lie almost parallel to bevelled edge, T3 very thin, inconspicuous, about 3 × length of terminal setules (difficult to see on some animals, Fig. 22H), T4 pinnate at apex of ramus, fine setules along bevelled edge between T3 and T4. Dorsal surface of ramus with network of ridges. Seta on first segment of antennule pinnate. Setation of mouthparts and ambulatory limbs typical of family. Antenna (Fig. 22A) with filiform setules on basis and segment 1 of endopod, exopod with five plumulose setae and one spinous seta, segment 2 of endopod with proximal setules, one small and two larger lateral setae, one plain and one annulate terminal seta, three geniculate setae with plain distal portion, terminal claw with blunt serrations. Mandible without setules on anterior lobe of palp. Maxillule similar to *P. tenuicaudus*, maxilla (Fig. 22B), maxilliped (Fig. 22F). P1 (Fig. 22C) exopod segment 1 with single crescentic row of denticles parallel to border, endopod with small triangular area of denticles at lateral end of fimbriate crescent, endopod l/w = 1.25. Serrulate spinous seta on segment 2 of P3 endopod thin, almost equal to length of endopod, large, serrate, spinous seta on segment 3 longer than endopod (1.5:1), (Fig. 23C). P4 endopod with massive, short, serrate, spinous seta on segment 2 and a similar serrate seta on segment 3 (Fig. 23B). P5 (Fig. 22D, E), dorsal (external) seta on baseoendopod long (40 µm), exopod lanceolate with blunt apex (w/l = 0.26 at level of lateral seta), ventral falciform ridge undulating, two pinnate dorsal setae, seta at apex pinnate, border setules filiform, long (25–30 µm), dorsal surface with network of ridges. Females carry 12 eggs in brood chamber (N = 7).

Adult males (Fig. 24A). Colouration, pits, network and striated hyaline border as described for female. Anterior outline of cephalosome rounded, slightly truncated with small convex projection in midline, lateral angle of antennule sockets with conical projection, rostrum V-shaped without ventral keel (Fig. 24D). Caudal ramus trapezoid (Fig. 23G), width greater than length (l/w = 0.9), medial edge straight, lateral edge slightly convex, posterior ⅓ of both edges with setules, α and β setae long (¾ width of ramus), terminal setae T1–T4 long, all pinnate, T3 larger than on female ramus, fringe of fine setules between T3 and T4. Antennule 43% of cephalosome width (Fig. 24A), segment 1 with pinnate seta, no ventral process on segment 3, segment 4 with small serrated triangular proximal denticle, medial large denticulate pad, distal denticle with double serrated edge (Fig. 24E), segment 5 of dactylus slender, cylindrical, ¾ length of segment 3+4, hooked distally (Fig. 24B), segment 6 small and fused with segment 5. Ambulatory limbs as for female except for following. P2 endopod with two plumose setae on terminal segment (Fig. 23D). P4 endopod segments 2 and 3 with long plumose setae (Fig. 23E). P5 acutely pointed trapezoid, setae long (⅔ length of lateral edge, first (lateral) seta pinnate with row of 7–8 ventral setules, remaining setae with 3–5 ventral setules (Fig. 23A). Spermatophore reinform with recurrent neck (Fig. 24F).

Remarks. The animals from Loch Hyne, Ireland, correspond to Claus' description of *Porcellidium scutatum*. For example, they are the same size and colour, the caudal rami are the same shape and have the same setation (Claus does not show T2, but as pointed out above this is hard to see on some specimens) and both have a long cylindrical dactylus on the male antennule. But the most compelling reason for regarding the two animals to be the same species is the unique hyaline border to the cephalosome. Claus states *"…surface at the edge of the cephalothorax with a clear outer margin set through with little rods"* (taf.VIII, abb.18). Figure 21F, G, H show the striated border of *Porcelloides scutatus*. Only two other species are known with a striated hyaline border, *Porcellidium akashimum* Harris and Iwasaki (1996a) and an undescribed Australian species of *Kushia*. The false border of *Tectacingulum tumidum* Harris, (1994) is striated, but the true hyaline border, which lies on the ventral side of the cephalosome, is not striated.

Superficially, the female of Claus' *Porcellidium scutatum*

looks very different from *Porcelloide tenuicaudus*. The caudal rami are not acutely pointed or excluded from the arch of the genital double-somite. However, two features show that Claus' *P. scutatum* belongs to the genus *Porcelloides*. The arrangement of denticles on the male antennule closely resembles that of *Porcelloides tenuicaudatus*, but differs from all other known species in the family. This together with the fact that two females from Loch Hyne carry eggs and an empty spermatophore on their P5 limb shows that Claus' *P. scutatum* should be assigned to the new genus as *Porcelloides scutatus* (Claus, 1889), comb. nov.

Distribution. Living specimens of this species were collected from a red alga (?*Gelidium*) in shallow water (10 to 40 cm) on the west side of Loch Hyne,Co. Cork, Ireland, in deep shade from overhanging trees, LH4.9.97, 11 ♀♀, 12 ♂♂, V. A. Harris 1997.

Claus (1889) collected this species from rocks and *Laminaria* in Trieste Harbour, Adriatic Sea, but it has not been recorded anywhere else since. It is not found on the coast of Ireland, or the west coast of England and Scotland. Its presence in Loch Hyne is surprising for it implies two widely separated isolated occurrences.

Loch Hyne (Ine) in County Cork, Ireland, is a deep tidal marine loch, about one square kilometre in area, situated about one kilometre inland. It is connected to the sea by a very narrow channel and rapids through which sea water flows at high tide on the coast. Tidal swing in the Loch is only a few centimetres. It supports an extremely rich marine fauna that includes many Mediterranean (Lusitanian) species not found elsewhere round the coast of Ireland, England or Scotland. The inland location of the Loch would protect it from the extreme weather of the open coast and this suggests it may contain a relic fauna from a period when the climate was warmer. The Loch's origin is uncertain but may represent a glacial lake that was replaced by sea water when sea-levels rose above the level of the rapids, due to changes in land or sea level. It is possible that *Porcelloides scutatus* represents a relic Lusitanian species that was once more widely distributed.

Animals belonging to *Porcelloides* have not been recorded from the Pacific region (Australia or Japan).

Discussion

The absence of a precise diagnosis for *Porcellidium viride* until now stems from the inadequacy of published descriptions and figures that has resulted in significant taxonomic confusion. This has led to wide difference of opinion among authors as to where the boundaries of the genus *Porcellidium* should be drawn.

There are two aspects to this problem. First there is the disagreement as to the synonymy of the species. Lang (1948) lumped together *P. fimbriatum* and *P. lecanoides* under the one name *P. viride* Philippi. Vervoort (1964) followed Lang and included *P. sarsi* under *Thyone viridis*. Bocquet (1948) recognized *P. lecanoides*, but renamed *P. fimbriatum* (*sensu* Sars 1904) as *P. sarsi*. Other authors recognize *P. fimbriatum* as a valid species. Harris & Robertson (1994) recognized *P. viride, fimbriatum* and *sarsi*, while Huys *et al*. (1996) recognized *P. fimbriatum, sarsi* and *lecanoides*. Walker-Smith (2001) and Wells (2007) recognize *P. viride, fimbriatum* and *lecanoides*. However, the detailed descriptions given above for *P. viride, P. fimbriatum* and *P. roscoffensis* clears up this uncertainty and shows that *P. sarsi* and *P. lecanoides* are synonyms for *P. viride*.

The second problem relates to the validity of new genera. Huys *et al*. (1996) reject five new genera proposed by Harris & Robertson (1994) and Harris (1994) on the grounds that new genera should not be erected until the genus *Porcellidium* had been settled, but they maintain that the family has only one genus *Porcellidium*. However, a number of their characters for the family are seriously inaccurate; for example, they maintain that the male antennule has five segments and is haplocer—features that would exclude all known species from the family.

Waker-Smith (2001) accepts that the family has more than one genus, but does not recognize five of the new genera and places them in *Porcellidium*. This move is recognized by Wells (2007). However, by doing this new characters are introduced into the diagnosis of *Porcellidium* that are not found in the type species, *P. viride*. Walker-Smith correctly asserts that new genera should be based on apomorphic characters and not unique combinations of characters.

In 1840 Philippi gave a diagnosis for a new genus, *Thyone*, for three new species, one of which he named *Thyone viridis*. From his drawing this appears to be a male stage IV copepodid belonging to the Porcellidiidae, but its shape is very strange and cannot be identified with any other known copepodid or adult within the family. Claus (1860) pointed out that *Thyone* was preoccupied and introduced the replacement generic name *Porcellidium* for his two new species, but he does not appear to recognize Philippi's *Thyone viridis* for he does not mention the name in any of his works.

However, Brady (1880) thought that one of his specimens was the same species as Philippi's animal and corrected the name to *Porcellidium viride* (Philippi, 1840). He gave a written description of a copepodid which he thought was the adult female of *P. viride*, but his illustration shows that it was a male copepodid.

Neither Claus nor Brady understood the significance of "mate guarding behaviour", where an adult male clasps a stage III, IV or V female copepodid with his antennules until the copepodid undergoes metamorphosis to an adult female. At that moment the male places his spermatophore on the nubile female. Adult males do not couple with male copepodids, consequently their P5s are easily seen—they terminate with six clearly visible setae. In contrast, the shape and setation of juvenile female P5s cannot be seen during the time they are clasped by the guarding male. As nearly all female copepodids are coupled to a male, the majority of free copepodids are males. Both Claus and Brady appear to have thought that P5s with six setae was a common feature of male and female animals and wrongly assumed that all copepodids, whether coupled or free, were adult females of the same species as the guarding male. Claus (1860), for example, labelled a male copepodid as the adult female of his *Porcellidium dentatum*; the true adult female, which is much larger and has differently shaped P5 limbs and caudal furca, he considered to be another species and named it *Porcellidium tenuicauda*. Similarly, Brady (1880) labelled a male copepodid "adult female", but the true adult female he incorrectly identified as another species—*Porcellidium fimbriatum*.

This confusion caused by sexual differences was further

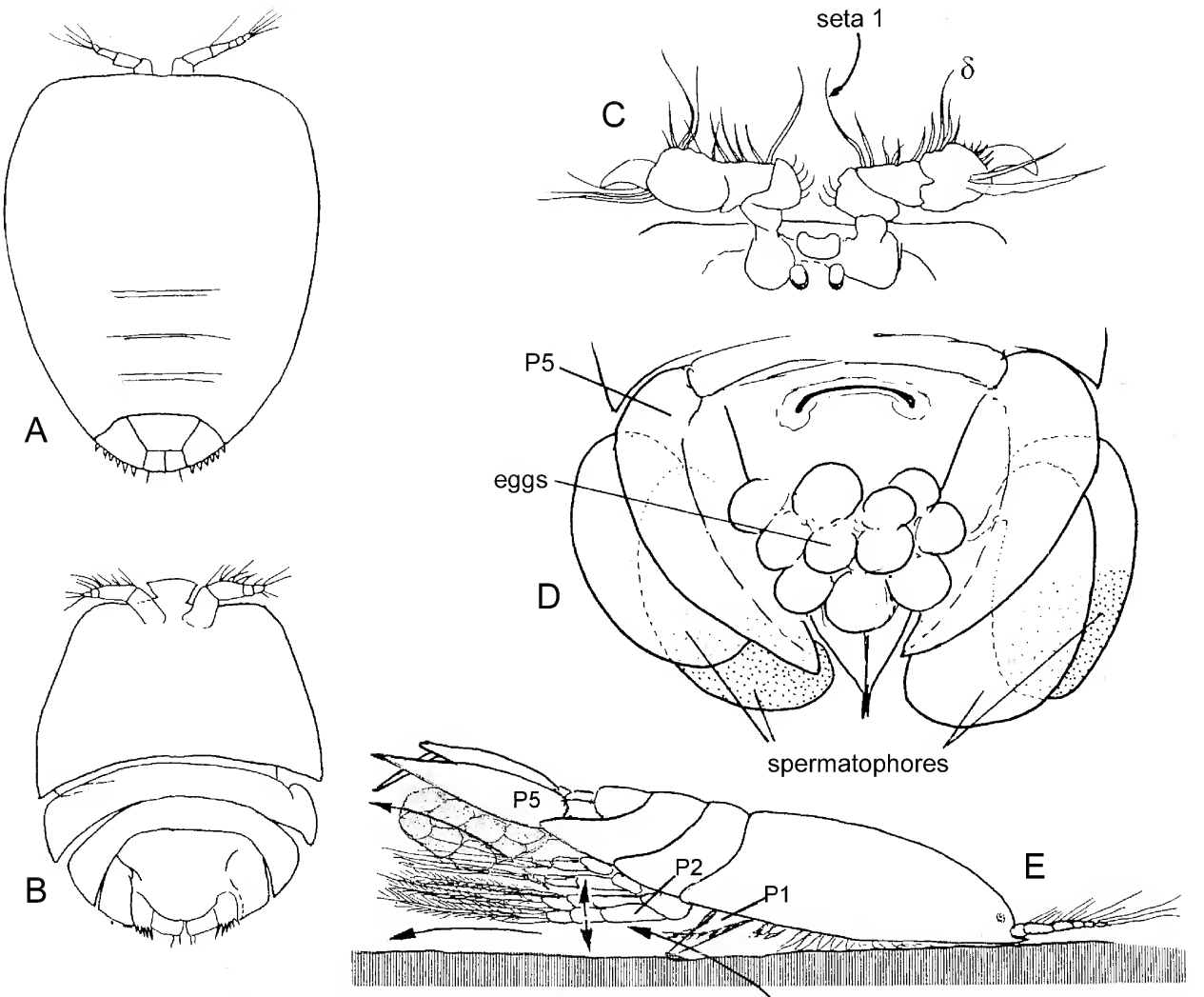

Figure 25. *(A)* Philippi's 1840 drawing of *Thyone viridis*. *(B)* Male copepodid labelled "female *Porcellidium viride"* (incorrectly identified as an adult female) Brady (1880). *(C)* P*orcellidium viride* male antennules (showing very long first seta on segment 2), Brady (1880). *(D) Porcelloides tenuicaudus* (Claus, 1860). Adult female with eggs and four spermatophores attached (freehand sketch of specimen in the NHM collection, V. A. Harris). *(E)* Female lifting body with P1 limbs to irrigate eggs.

complicated by wrong identification of animals. Claus (1889) acknowledges that his *P. dentatum* is really the male of *P. tenuicauda*, but his (1860) drawing of male *P. dentatum* is of a male *P. fimbriatum*. Similarly, Brady's 1880 drawing of *P. fimbriatum* is clearly the adult female of *P. viride*.

From this confusion and the absence of accurate description it is not surprising that later authors disagree on the true identity of *P. viride* and the diagnostic characters of the genus *Porcellidium*.

The confusion between "*viride*", "*fimbriatum*", "*lecanoides*" and "*sarsi*"

Brady thought that the large females in his collection were a different species to his *P. viride* and identified them as *P. fimbriatum* Claus, 1863, but Claus' description is not very clear and his illustrations do not show a single species specific character that would have enabled Brady to identify his animals correctly. The most obvious difference between the two species is the placement of the β caudal seta, but this is not shown by either Brady or Claus. A revised description of *P. fimbriatum* was given by Claus (1889) in which at least eight specific characters are mentioned or illustrated. This showed clearly that Brady's female was the adult female of *P. viride* and not *P. fimbriatum.* Paradoxically, Claus makes the mistake of stating that both Brady's *P. fimbriatum* and *P. viride* are synonymous with his *P. fimbriatum* 1863.

In the present study, samples collected from *Laminaria digitata* at Clachan, Seil Sound Oban, Scotland were found to have two distinct species living on the same seaweed, [Brady (1880) collected some of his specimens of *P. viride* at Loch Fyne, near Oban, Scotland]. They are easily distinguished by their colouration and size. Adult males of the larger species have an unusually long first seta on segment 2 of the antennule (it is about 2½ times the length of seta 2 and 3, Fig. 7G). This is a unique species specific character that has not been found on any other known member of the Porcellidiidae. Brady's illustration of the antennules of his adult male *P. viride* shows the same long first seta (Fig. 25C), therefore, the larger male animals from Scotland must be *P. viride.* The corresponding larger females clearly resemble Brady's illustration of *P. fimbriatum* which must be the adult female of *P. viride*. It is of interest to note that animals from Norway identified by Sars (1904) as *P. fimbriatum* (and

renamed *P. sarsi* by Bocquet in 1948) have the same long first seta on segment 2 of the male antennule and must be *P. viride*. Claus' (1889) description of *Porcellidium lecanoides* does not show the male antennule, but he illustrates five other species specific characters which show his animals are *P. viride*, thus, *P. lecanoides* and *P. sarsi* are junior synonyms for *Porcellidium viride*.

The second species found in the samples from Clachan, Scotland, is smaller and distinguished by a dark blue stripe down the back (Plate 1C,E, p. 67). Comparison of these with *P. viride* from the same locality show that the first seta on segment 2 of the male antennule (Figs 12D) is not much longer than the second or third seta, moreover, details of the female genital double-somite (Fig. 6E) and caudal rami (Fig. 6D) are very different and conform to Claus' (1889) description of *Porcellidium fimbriatum*.

The "*ovatum*" problem

Porcellidium ovatum Haller, 1879 and *P. scutatum* Claus, 1889 have caused problems even to this day because of Haller's poor description. Lang (1948) and Wells (2007) consider them synonymous, but Bodin 1997 does not list either (presumably because he considers both synonymous with Claus' *Porcellidium tenuicauda*). The illustration Haller (1880) gives of *Porcellidium ovatum* Haller, 1879 shows a remarkable resemblance to *Porcelloides tenuicaudus.* It is not clear why Haller (1879) regarded his animal as a separate species, but the body proportions of Claus' (1860) original drawing appear distorted and not obviously egg-shaped. This, together with the apparent difference in shape of the caudal rami, may have led Haller (1879) to regard them as different species. The caudal rami on most preserved specimens of *Porcelloides tenuicaudus* are depressed and appear short in dorsal view, just as Haller (1880) shows in his illustration, but when dissected and laid flat the rami are elongate as shown by Claus (1860).

Monard (1935) states *Porcellidium ovatum* is identical to *Porcellidium tenuicauda,* but gives no evidence for this. There are, however, good reasons for accepting his opinion. Both Claus (1863) and Haller (1879) record a length of 1.3 mm. This is unusually large for members of the Porcellidiidae and is only exceeded by two other species: *Dilatatiocauda bipartita* (Kim & Kim, 1997), 1.45 mm and *Murramia magna* Harris, 1994, 1.38 mm. Haller (1880) describes his animal as "egg-shaped" in outline (hence the trivial name *ovatum*), but *Porcelloides tenuicaudus* is also "egg-shaped" or ovoid, although this is not obvious from Claus' (1860) drawing (the "egg shape" is more obvious when the animal conglobates).

Most members of the Porcellidiidae are coloured or have a colour pattern, due to the colour of the chitinous exoskeleton and/or pigment localized immediately under the cuticular exoskeleton, but *Porcelloides tenuicaudus* shows a marked departure from this arrangement. Specimens from Scotland contained a large number of dark orange or brown oil droplets in the haemocoel that gave the animals an orange or reddish-brown colouration (these are lost in spirit preserved specimens). In his description of *Porcellidium ovatum,* Haller (1880) states that the animals are coloured due to the presence of red and yellow fat globules in the body that glitter through the colourless cuticle. It should be noted that *Porcelloides scutatus*, the only other egg-shaped European species, does not have oil droplets and its dorsal red patch is due to sub-cuticular pigment. However, by far the most compelling reason for regarding *Porcellidium ovatum* synonymous with *Porcelloides tenuicaudus* is the presence of two reniform spermatophores on the female's P5 limbs shown in Haller's (1880) illustration. Claus (1860) and Bartsch (1987) both show two reniform spermatophores in their illustrations of *Porcellidium tenuicauda.* This is in contrast to the rest of the Porcellidiidae where only one spermatophore is deposited on a female and this only stays attached for a matter of hours.

Lang (1948) treats *Porcellidium scutatum* Claus, 1889 and *Porcellidium acuticaudatum* Thompson & Scott, 1903 as synonyms for *P. ovatum* Haller, 1879, thus, anyone using Lang's key will misidentify *Porcelloides scutatus* as *Porcellidium ovatum*. Three other species have been misidentified through Lang's key. Geddes (1968) referred animals from Barbados to *P. ovatum*, but they do not show any of the characteristics of *Porcelloides tenuicaudus* and probably belong to *Acutiramus.* Holmes & O'Connor (1990) referred specimens in the NMI of *Porcelloides scutatus* collected from Loch Hyne by D. Minchin (July 1982) to *Porcellidium ovatum*. Animals from Oshoro Bay, Hokkaido, Japan (Kito 1977) and Guandong Province, China (Zhang & Li 1976) both referred to as *P. ovatum* are unlikely to belong to that species. The porcellidiid fauna of Japan is reasonably well known but the genus *Porcelloides* has not been recorded from that region. It is probable that the animals from Hokkaido and Guandong are a species of *Kensakia* because the caudal rami of *Porcelloides* and *Kensakia* are superficially similar. Anyone using Lang's (1948) key for identification would misidentify species of *Kensakia* as *P. ovatum. Porcellidium acuticaudatum* almost certainly belongs to *Kensakia.*

Haller (1879) described another species, *Porcellidium parvulum*, also from Messina, which he illustrated the following year, Haller (1880). One of his animals appears to be a stage III or IV female copepodid (it does not have typical stage V P5 limbs and is only 0.55 mm). The other animal is a male but its antennules are not transformed and therefore it is not an adult. With a body length of 0.71 mm, it is likely to be a stage IV or possibly stage V male copepodid. The large size of these juveniles suggests they belong to *Porcelloides tenuicaudus*, but their identity cannot be established with certainty from Haller's (1880) description.

Reproductive biology of Porcellidiidae

Perhaps the most significant fact revealed through study of the European species is a fundamental difference in the reproductive biology between *Porcelloides tenuicaudus* and all other members of the Porcellidiidae.

From observations on living animals in Scotland and Australia it was found that shortly after metamorphosis an adult male will seek and couple with a juvenile female copepodid (usually stage II or III) by clasping the posterior region with his antennules. This coupling has been referred to as mate guarding behaviour, Huys & Boxshall (1991). Each time the female copepodid moults to the next stage the guarding male re-couples with it until stage V is reached. About this time the spermatophore develops in the male. The spermatophore of *Porcellidium viride* is typical of nearly all members of the family. It is a long tubular sac (sausage-

shape) with a narrow neck. About ¾ of its volume is occupied by the sperm mass, the remainder is a clear fluid. The guarding male re-couples with the newly metamorphosed female, as she emerges from the final moult, to deposit his spermatophore on her body. Usually it is placed on the ventral side of the females genital double-somite, but it may be placed anywhere on the dorsal or ventral part of the posterior body. Only part of this activity has been observed on one occasion with *P. hormosirii* (personal observation). Whilst clasping the female in the usual manner, the male pushed the hind region of its body forward under the female that appeared to be lifting her body as she does when irrigating eggs (Fig. 25E). The spermatophore, when deposited, adheres by its neck end (presumably by the congealed clear fluid) and remains attached for a relatively short period, an hour or so, before the empty case is lost. During that time the spermatozoa migrate to the spermathecae. When filled with sperm the spermathecae can usually be seen through the transparent cuticle of the nubile female before it hardens and colouration develops. The empty spermatophore case is lost long before egg-laying starts. Females receive only one spermatophore during their life span.

Although the reproductive behaviour of *Porcelloides tenuicaudus* has not been observed and no coupled specimens were found in the very small sample available for study, there is a striking difference in the pattern of insemination between this genus and that outlined above. Mature males have typical antennules modified for clasping and, like all other members of the family, carry only one spermatophore. But the shape of the spermatophore and its placement on the female is quite different. It is common to see female *P. tenuicaudus* carrying two or more spermatophores. This must indicate that more than one male has deposited a spermatophore on the same female.

The spermatophore, when deposited on the female is a large bean-seed or kidney-shaped (reniform) sack with a recurrent neck or duct running along the concave side. It is firmly attached to the dorsal surface of the female's P5 lying on its side, (on some animals the recurrent duct can be seen lying in the gap between P5 and genital double-somite). The original drawing by Claus (1860) is ambiguous: he shows two spermatophores connected by ducts to the spermatheca, but it is not clear whether they are dorsal or ventral to the P5 limb.

Perhaps the most significant feature in the reproductive biology of *P. tenuicaudus* is multiple deposition of spermatophores on the female. Claus (1860), Haller (1880) and Bartsch (1987) all show two spermatophores, one on each P5, but Bocquet (1948) states that there may be two, three or four. The female shown in Fig. 17A and Plate 1G (p. 67) has two spermatophores attached to the P5s, but a specimen of *Porcelloides tenuicaudus* in the NHM, London carrying eggs has four spermatophores attached (Fig. 25D), (personal observation). Because a male only produces one spermatophore, the presence of more than one on a female implies that the female has received them from more than one male. The fact that a female of other species only receives one spermatophore during her life time (immediately after metamorphosis) and males never couple with adult (egg bearing) females implies that the normal mate guarding behaviour and the stimulus inducing release of the spermatophore is different in *Porcelloides* to all other species.

Spermatophores remain attached for a long period. This is indicated by two facts. First empty spermatophore cases are sometimes covered in the same epizoic micro-organisms (diatoms, suctorian protozoa etc.) found on the female's body and second, empty cases are still present on females carrying eggs.

These reproductive peculiarities appear to be of more fundamental significance than normal apomorphic differences and set *Porcelloides* apart from all other genera. This might be considered grounds for splitting the family into two sub-families, but a far more detailed study of the reproductive biology of *Porcelloides* is necessary before such a step is taken. Except for its own apomorphies, *Porcelloides* shares all the characteristics of the Porcellidiidae.

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Appendices

Appendix 1. Identity of specimens in the Norman slide collection Natural History Museum, London (339 Porcellidiidae).

Twenty microscope slides of specimens collected by A. M. Norman over a period from 1861 to 1906 are of interest because they contain type specimens of his *Porcellidium subrotundum* and reflect the nomenclature of that period. Unfortunately identification is difficult because the slides are in very poor condition, but several of the specimens can be positively identified. Norman based his identifications on Claus' 1863 description of *P. fimbriatum*. The following criteria have been used to separate the species

Porcellidium viride
body shape L/W ≤ 1.5
caudal ramus l/w ≤ 2.2
$M_1/M_2 < 0.9$ (where M_1 = α to β, M_2 = β to γ); diatoms usually present

Porcellidium fimbriatum
body shape L/W > 1.7
caudal ramus l/w ≥ 2.7
$M_1/M_2 > 2.5$

reg. number	label	identification
1951.8.10.892	*Porcellidium tenuicauda.* Washed off dredged weed, Ventry Bay. 1 ♂ *P. fimbriatum* 1 ♂.	*Porcelloides tenuicaudus.* *Porcellidium viride.* CR. l/w = 1.9.
1951.8.10.894	*P. tenuicauda* Claus. In bulb of *Laminaria bulbosa* Roundstone, 1865.	*Porcelloides tenuicaudus.*
M2609	*P. tenuicauda* Claus. Gurnsey.	*Porcelloides tenuicaudus.*
M2566	*P. lecanoides* Claus. Plymouth, 1889.	*Porcellidium fimbriatum.* CR. l/w = 2.7: terminal setae pinnate, genital double-somite cleft.
1900.3.6.706	*P. fimbriatum* Claus. = *viride* Phil? Shetland, 1861.	*Porcellidium viride,* 3 ♀♀. Covered in diatoms. L/W 1.3; l/w 1.6; $M_1/M_2 = 0.8$.
M2565	*P. fimbriatum* Claus. Hillswick, Shetland, 1867.	Poor slide. Diatoms++. Probably *Porcellidium viride*.
M2613	*P. fimbriatum* Claus. Hillswick, Shetland, 1867.	*Porcellidium viride* (males). Male with purple patch on cephalosome. Many male copepodids.
M2614	*P. fimbriatum* Claus. Male *dentatum* + junior; Hillswick, Shetland, 1867.	*Porcellidium viride* (copepodids).
1900.3.6.707	*P. fimbriatum* Claus. 1 ♂ and 3 ♀♀ Tide marks. Oban, 1877.	*Porcellidium viride.* Poor slide, diatoms ++
M2611	*P. fimbriatum* Claus. Male *P. dentatum* Cl. Oban, 1877.	*Porcellidium viride*. (5 poor ♀♀ and copepodids). Diatoms++, $M_1/M_2 = 0.88$, CR. l/w = 2.0.
M2612	*P. fimbriatum* Claus. Oban, 1877.	Males. Poor slide, probably *Porcellidium viride.*
M2564	*P. fimbriatum* Claus. Firth of Clyde, 1862.	*Porcellidium viride.* Diatoms ++, $M_1/M_2 = 0.57, 0.68$.
M2610	*P. fimbriatum* Claus = ?*viride*. Catwater, Plymouth, 1889.	Probably *Porcellidium viride.* Male covered in diatoms.
M2615	*P. fimbriatum* Claus. Rock pools, Plymouth, 1889.	Two females, poor specimens with diatoms. Probably *Porcellidium viride.*
1900.3.6.708	*P. fimbriatum* Claus. Males and females. Tobermory, Mull, 1866.	All *Porcellidium viride.* Diatoms ++
1900.3.6.709	*P. fimbriatum* Claus. Males. Florö, Norway, 1882.	Poor slide. Mostly copepodids of *Porcellidium viride.*
M2608	*P. lecanoides* Claus. Guernsey, 1906.	*Porcellidium viride.*
M2607	*P. subrotundum.* Norman types = *P. fimbriatum* junior. Hillswick, Shetland, 1867.	Seven copepodids, some with patch of purple on posterior cephalosome. All appear to be *Porcellidium viride.*
1951.8.10.893	*P. subrotundum* and *P. dentatum.* On *Laminaria.* Hillswick, Shetland.	All copepodids of *Porcellidium viride.*

Appendix 2. Identity of specimens of Porcellidiidae in the National Museum of Ireland, Dublin.

catalogue description	locality where found	identification
Porcellidium fimbriatum	Discovery Bay, Jamaica	Unidentified, but not *P. fimbriatum* Claus 1863
P. lecanoides Claus	Achill, Co. Mayo	*Porcellidium viride*
P. ovatum Haller	Loch Hyne, Co. Cork,	*Porcelloides scutatus* (Claus, 1889) comb. nov.
P. ovatum, *sensu* Geddes	Discovery Bay, Jamaica	*Acutiramus geddesi* (Geddes, 1968) comb. nov.
P. sarsi Bocquet	Loch Hyne, Co. Cork; Co. Dublin; Co. Galway	*Porcellidium viride*
P. tenuicauda	Loch Hyne, Co. Cork	*Porcelloides tenuicaudus* (Claus, 1860) comb. nov.

Note. Slide and spirit specimens in the NMI collection do not have individual registration numbers to identify them.

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Porcellidiidae of Australia (Harpacticoida, Copepoda). II. The Importance of the Male Antennule in Taxonomy

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Abstract. Nine new species belonging to the Porcellidiidae are described from Queensland and New South Wales, Australia. Two new genera *Ravania* gen. nov., and *Synurus* gen. nov., have been erected to accommodate three new species from Queensland, *Ravania wellsi* sp. nov., *R. doliocauda* sp. nov., and *Synurus ctenocheirus* sp. nov. Two other new species, *Acutiramus bipunctatus* sp. nov., and *Kensakia australis* sp. nov., are also described from Queensland. Four new species are added to the New South Wales list, *Kushia spathoides* sp. nov., *Acutiramus edenensis* sp. nov., *A. cumulus* sp. nov., and *A. iwasakii* sp. nov. A Japanese species, *Clavigofera pacifica,* is recorded from NSW. This brings the total number of species known for the East coast of Australia to 30. The importance of the male antennule in taxonomy of the family is discussed.

Keywords: Porcellidiidae, *Porcellidium, Ravania, Synurus*.

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Twenty species of Porcellidiidae have been described from New South Wales and Victoria, but none from Queensland, Australia. They were placed in seven genera (*Porcellidium* and *Acutiramus*, Harris & Robertson (1994), *Tectacingulum, Murramia, Kioloaria* and *Brevifrons* Harris, (1994) and *Dilatatiocauda*, Harris (2002), however, Walker-Smith (2001) placed *Acutiramus*, *Murramia* and *Kioloaria* in *Porcellidium* on the grounds that they were not based on apomorphic characters. This confusion arose from the fact that the type species for *Porcellidium* had never been adequately described. The re-description of *Porcellidium viride* (see Harris, 2014) has enabled a definitive diagnosis to be given for the genus and the validity of all the proposed genera to be reassessed. The species recorded from South Australia by Nicholls (1941) are not considered here because his descriptions are inaccurate and do not allow positive identification.

The present account describes five new species from Queensland. Two of these share many features with *Porcellidium ravanae* Thompson & Scott, 1903 which was re-described by Wells & Rao (1987). Some of their characters appear to be apomorphic. This excludes them from *Porcellidium* and so it is proposed to place them in a new genus, *Ravania* gen. nov. A third Queensland species resembles *Porcellidium unicus* Ummerkutty, 1970. They both share a number of apomorphic characters which exclude

them from *Porcellidium*. It is proposed that these animals are placed in a new genus, *Synurus* gen. nov. The genus *Acutiramus* is redefined and maintained to accommodate a new species from Queensland, *A. bipunctatus*, and three new species from NSW, *A. edenensis, A. cumulus* and *A. Iwasaki*. Two new species are described, *Kensakia australis* from Queensland and *Kushia spathoides* from NSW which belong to genera previously only known from Japan and Korea.

The Japanese species, *Clavigofera pacifica* Harris & Iwasaki, 1996, is recorded in Australia for the first time.

A survey of 50 Australian and Japanese species, for which detailed information about the structure of the male antennule is known, has shown that this appendage offers more useful taxonomic characters than any other part of the body. Not only do they show species specific characters that positively identify each species, but the overall configuration of shape, type and placement of setae and the shape, number and position of the coupling denticles is characteristic for each genus. Consequently the male antennule has far greater importance in porcellidiid taxonomy than the structure of the genital double-somite, caudal rami and P5 limbs that provided characters upon which specific differences were previously based, Lang (1948), Huys *et al.* (1996).

Because of this, male specimens have been chosen for the holotype for each of the new species named here. The variety of male antennule structure will be shown in the following descriptions of new species and their significance outlined in the General Discussion.

Methods and terminology

Methods and terminology follow Harris & Robertson (1994) and Harris (2014). The male antennule is examined and measured from the ventral side when fully extended. The following method is used to obtain animals in this condition. Animals are washed from seaweed in a 50/50 mixture of water saturated with CO_2 (from a soda siphon or bottled soda water) and tap water. This appears to anaesthetize or immobilize the animals with antennules extended. Whilst in this state they are fixed with dilute formalin (2–5% formaldehyde) and later preserved in 5% borate buffered formalin (this retains the animal's colouration for a year or more).Two measurements of body length are given: L_{max} from rostrum to posterior extremity of the caudal rami, and L_{urs} from rostrum to posterior extremity of the genital double-somite.

Drawings, biometric data and description of each species are based on calibrated digital photographs of paratype specimens mounted on slides in 50% glycerol or dissected and mounted in polyvinyl lacto-phenol (PVLP).Over a period of many years PVLP tends to over-clear specimens, but this can be overcome by using phase optics.

The relative position of the α and β setae on the caudal ramus is indicated by the Hicks' index defined as the distance of the seta from the posterior extremity of the caudal ramus divided by the length of the ramus expressed as a percentage (i.e., α/ramus length × 100).

The naming of setae on the male antennule (δ, π, σ, τ) is illustrated in Fig. 29E.

Abbreviations: NHM, Natural History Museum, London; AM, Australian Museum, Sydney, NSM, National Science Museum, Tokyo (now National Museum of Natural Science, Tokyo). All holotype, allotype and paratype specimens of the new species described in this paper have been deposited in the Australian Museum, Sydney. Paratype specimens of each species have been deposited in the Natural History Museum, London. Type series and samples of most of the species are currently held by the author, but will be deposited in AM, Sydney. Were possible named specimens will be deposited in other Australian Museums.

Systematics

Family Porcellidiidae Boeck, 1865

Genus *Ravania* gen. nov.

Porcellidium.—Thompson & Scott, 1903: 275.—Wells & Rao, 1987: 29; Bodin, 1997: 65; Walker-Smith, 2001: 656; Wells, 2007: 79.

Type species. *Ravania wellsi* sp. nov.

Diagnosis. Male antennule segment 3 with single denticle at base of anterior process (not comb-like), segment 4 with two tooth-like coupling denticles, no brush-pad or denticulate pad present; anterior of male cephalosome semicircular in outline (not truncated), rostrum oval in ventral view; female cephalosome not truncated; female caudal ramus not rectangular, T1 lateral, posterior border between T1 and T4 rounded or obliquely convex; terminal seta T2 always present, T3 always absent from male and female caudal ramus; female genital double-somite short, narrow (about ½ width of cephalosome), pointed posteriorly, not clearly divided into anterior and posterior lobes; maxillule endopod with six setae; coxal lobes of maxillipeds touch in midline; female P5 exopods without ventral expansion, extend beyond genital double-somite, but do not touch posteriorly; male P5 trapezoid with one lateral and five terminal setae; spermatophore elongate, ephemeral on female, multiple insemination does not occur.

Species composition. *Ravania ravanae* (Thompson & Scott, 1903) comb. nov.; *Ravania wellsi* sp. nov.; *R. doliocauda* sp. nov.

Members of genus known from Indian Ocean (Sri Lanka), sub-tropical coast of Queensland and northern coast of NSW, Australia.

Etymology. The specific name *ravanae* has been raised to generic rank as *Ravania* (feminine).

Remarks. The arrangement of denticles on the male antennule, rounded anterior to male cephalosome, shape of the female genital double-somite and caudal ramus which lacks T3 are features that distinguish *Ravania* from *Porcellidium* and *Acutiramus*. From the re-description of Wells and Rao (1987) it is clear that *Porcellidium ravanae* belongs to *Ravania* and should be renamed *Ravania ravanae* (Thompson & Scott, 1903) comb. nov.

The description by Wells and Rao (1987) lacks important information about the male antennule and their illustration labelled "female P4" appears to be the male limb, however, it is clear that *R. ravanae* and *R. wellsi* are two distinct species. They differ in the following important details: *R. ravanae* has a small patch of setules on anterior lobe of mandibular palp, border setules on anterior lobe of female genital double-somite, T2 on the caudal ramus is very short and the male P2 endopod has three terminal setae.

Key to the species of *Ravania*

1 Female caudal furca "dolioid" (barrel-shaped), rami not rhomboid. (Plate 1E,F, p. 163) ..... *Ravania doliocauda* sp. nov.

—— Female caudal furca pointed, rami rhomboid with T4 at rounded apex 2

2 Anterior half of female genital double-somite without border setules. Male P2 endopod with two terminal setae. Short rows of setules at base of each terminal seta on male P5. (Plate 1A,B) ..... *Ravania wellsi* sp. nov.

—— Anterior half of female genital double-somite with border setules. Male P2 endopod with three terminal setae. No setules at base of each terminal seta on male P5 ..... *Ravania ravanae* (Thompson & Scott, 1903) comb. nov.

Ravania wellsi sp. nov.

Figs 1–4, Plate 1A

Type material. HOLOTYPE adult male, length 0.51 mm, P81198; ALLOTYPE adult female, length 0.58 mm, P81199; PARATYPE specimens, 5 ♀♀, 3 ♂♂, 3 juveniles, P81200, deposited at AM, Sydney. Additional paratypes deposited at NHM, London. All collected from *Eucheuma denticulatum*, sublittoral fringe, Point Vernon, Hervey Bay, Queensland (25°15'S 152°47'E), V. A. Harris, 1998.

Diagnosis. Male antennule with short pointed spur or thorn-like denticle at base of δ seta on segment 3; anterior half of female genital double-somite without border setules, posterior half with border setules, no seta in lateral indentation between anterior and posterior lobes, half caudal ramus contained in arch of genital double-somite; female caudal ramus rhomboid, terminal seta T2 almost as long as γ seta; male P2 with only two terminal plumose setae on endopod segment 3; female P4 with two spinous setae on endopod; female P5 exopod with one dorsal and two apical setae; male P5 with short rows of ventral setules at base of each terminal seta.

Biometric data. *Females* (N = 29): maximum length (L_{max}) mean 0.57 mm, range 0.54–0.61 mm, body length (L_{urs}) mean 0.52 mm, range 0.49–0.56 mm; cephalosome width (W) mean 0.36 mm, range 0.34–0.44 mm; rostrum width 0.08 mm; width of genital double-somite 0.23 mm, length 0.14 mm, arch 0.08 mm; caudal ramus 0.115 mm, width 0.042 mm.

Ratios: L_{urs}/W 1.44, W/R 4.5; genital double-somite w/l 1.65, arch 57% of length; caudal ramus 22% of L_{urs}, ramus l/w 2.7, Hicks' index for β 68%.

Males (N = 23): length (L_{max}) mean 0.51 mm, range 0.49–0.54 mm, body length (L_{urs}) mean 0.48 mm, range 0.46–0.51 mm; cephalosome width 0.35 mm. antennule (N = 3, fully extended 0.125 mm; spermatophore 0.18 × 0.065 mm.

Ratios: L_{urs}/W 1.4; antennule 24.5% of L_{urs}, antennule segment 2 31%, segment 3+4 35%, dactylus 21% of antennule length; spermatophore 37% of body length L_{urs}.

Description. *Adult females* (Fig. 1A; Plate 1A, p. 163): colouration, pale red with central cephalosome and metasome segments 1 and 2 deep red, metasome segments 3 and 4 pale red, genital double-somite and caudal rami deep red. Some animals are pale red or colourless. Eye spot dark brown. Anterior of cephalosome broadly rounded, rostrum prominent, narrow with hyaline anterior border. Dorsal surface ornamented with pits (4 μm). Hyaline border 8 μm wide, without striations. Sensillum on epipleural lobe of second metasome segment conspicuous, longer than other species. Labrum without central patch of setules or ridge plates. Genital double-somite (Fig. 1E) with slight indentation that marks the boundary between anterior and posterior lobes, anterior lobe short, convex, with thickened edge but no setules, posterior lobe triangular, pointed posteriorly with border setules. Arch of genital double-somite deep, encloses about half length of caudal ramus, dorsal surface with pits. Genital opening as in Fig. 1F. Caudal rami (Fig. 1D) rhomboid, length about 2½ times width, sides almost parallel, oblique posterior edge slightly convex, apex broadly rounded with pinnate T4. Dorsal surface with prominent network of ridges, β seta ⅓ way down ramus, γ seta about ½ way along oblique edge. Medial edge with border setules up to the level of β seta, lateral edge slightly convex with border setules distally, T1 unipinnate at lateral corner of oblique edge, T2 plain about as long as γ seta, T3 absent, posterior border with fine setules from T1 to T4. Structure and setation of mouthparts and ambulatory limbs typical of family. Antenna (Fig. 2A) exopod with five plumulose setae and one finely serrulate spinous seta, endopod segment 2 with two lateral setae, geniculate setae with plain end segment, claw fine comb-like. Mandible (Fig. 2D, E, F) without setules on anterior lobe of palp. Maxillule (Fig. 2B), endopod with six setae, exopod with one bulbous seta. Maxilla (Fig. 2H) and maxilliped (Fig. 2G) typical. No area of denticulate setules on P1endopod (Fig. 2C). Serrulate spinous seta on segment 3 of P2 endopod about ½ length of endopod (Fig. 3C). Serrulate spinous seta on segment 2 of P3 endopod (Fig. 3A) shorter than endopod (0.8:1), large serrate spinous seta on segment 3 longer than endopod (1.3:1). Internal seta on segment 2 and segment 3 of P4 endopod strong spinous, other setae plumose (Fig. 3F). Dorsal surface of P5 exopod with pits, internal seta on baseoendopod serrulate, about ½ length of exopod, exopod lanceolate with one dorsal seta and two apical setae (Fig. 3E). P5s reach beyond genital double-somite to extremity of caudal rami, but do not touch posteriorly. Females carry six large eggs.

Adult males (Fig. 1B; Plate 1B, p. 163). Colouration similar to female, but posterior region of most specimens is pale red or colourless. Anterior of cephalosome rounded (not truncated), rostrum projects anteriorly, in ventral view rostrum appears

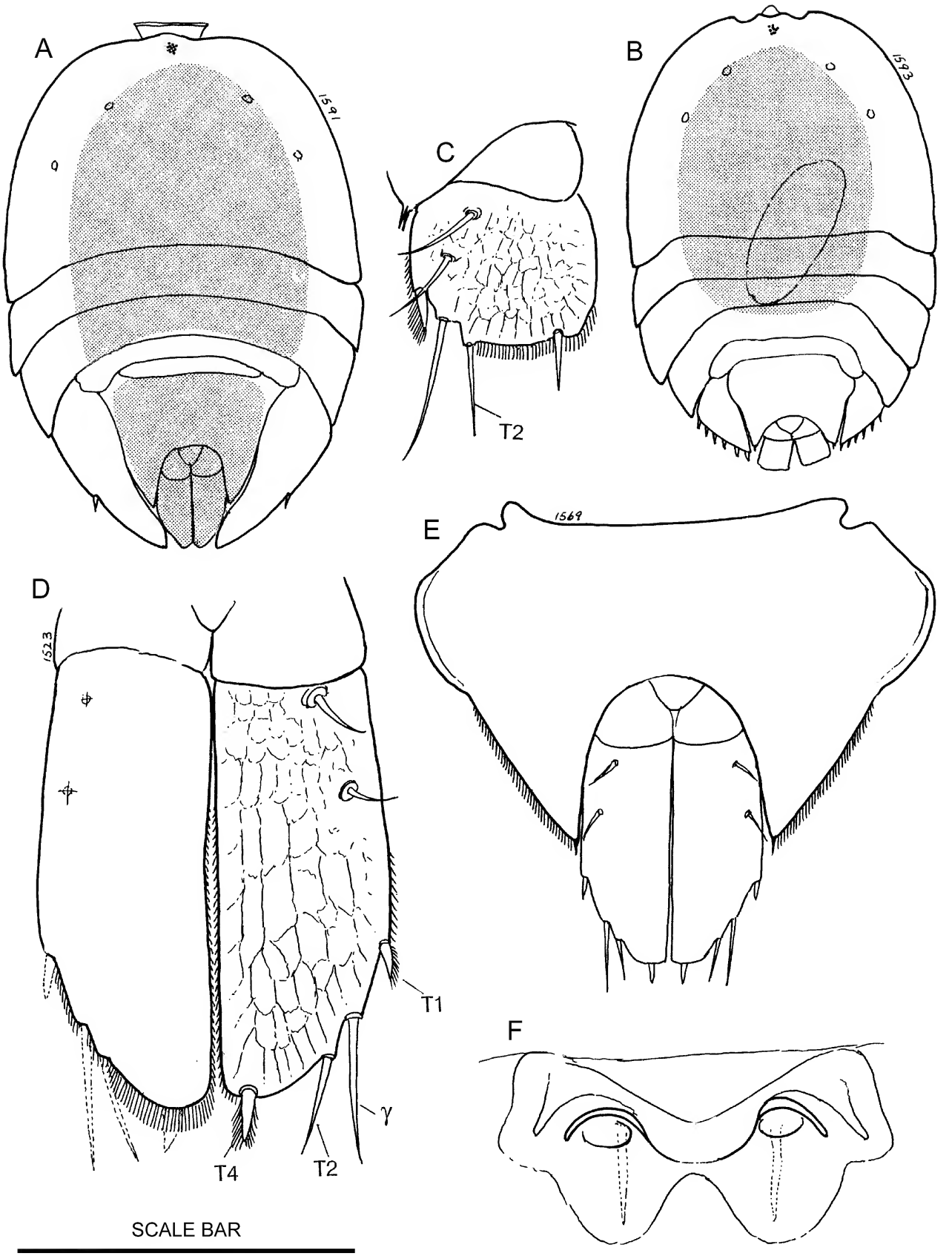

Figure 1. *Ravania wellsi* sp. nov. Female: *(A)* adult; *(D)* caudal ramus (left ventral, right dorsal); *(E)* genital double-somite and caudal rami; *(F)* genital opening. Male: *(B)* adult; *(C)* caudal ramus. Scale bar: A, B = 0.37 mm. C, D = 0.08 mm. E = 0.15 mm. F = 0.06 mm.

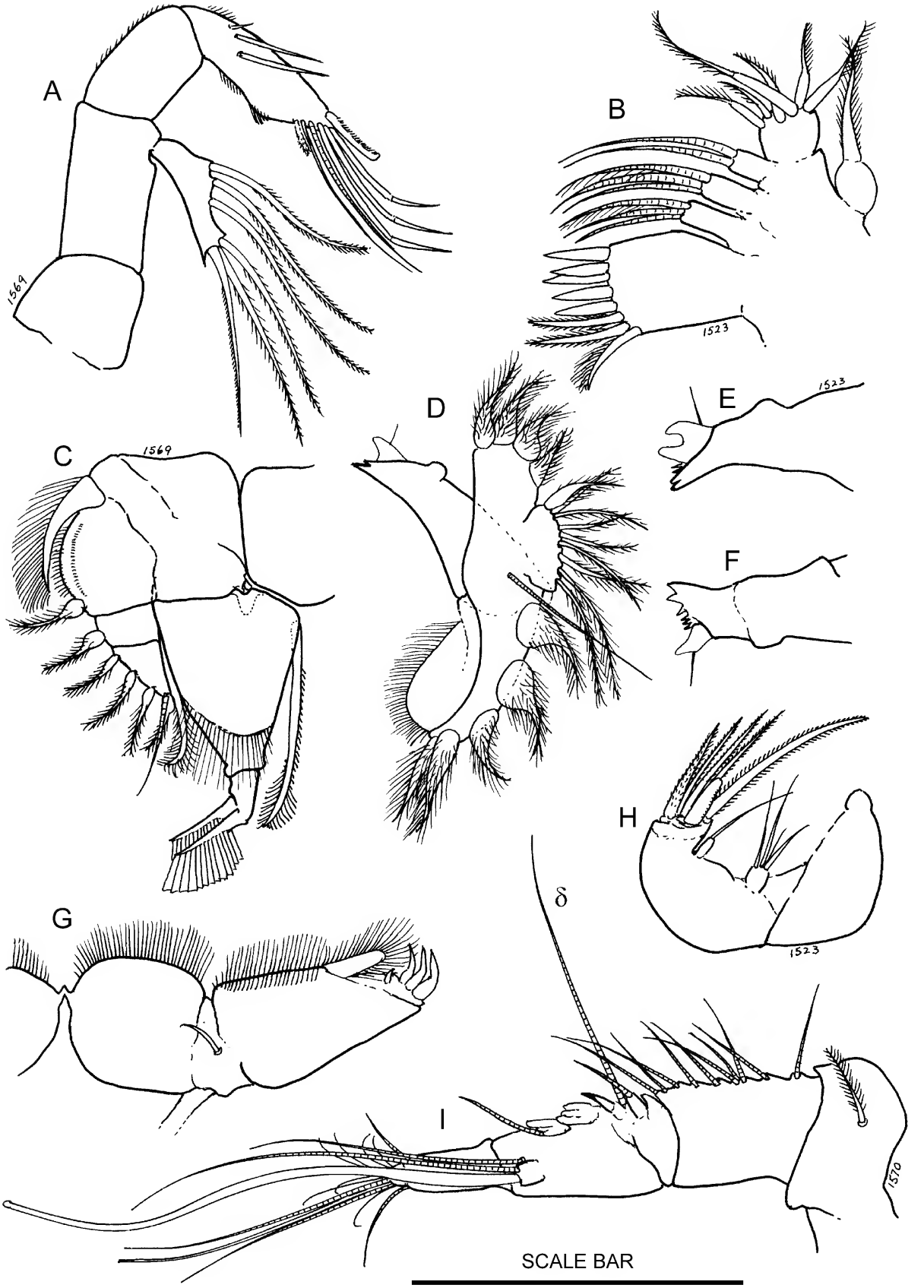

Figure 2. *Ravania wellsi* sp. nov. Female: *(A)* antenna; *(B)* maxillule; *(C)* P1; *(D)* mandible; *(E, F)* left and right molar process; *(G)* maxilliped; *(H)* maxilla. Male: *(I)* antennule (ventral). Scale bar: A, I = 0.08 mm. B = 0.06 mm. C, D = 0.14 mm. E, F, H = 0.1 mm. G = 0.12 mm.

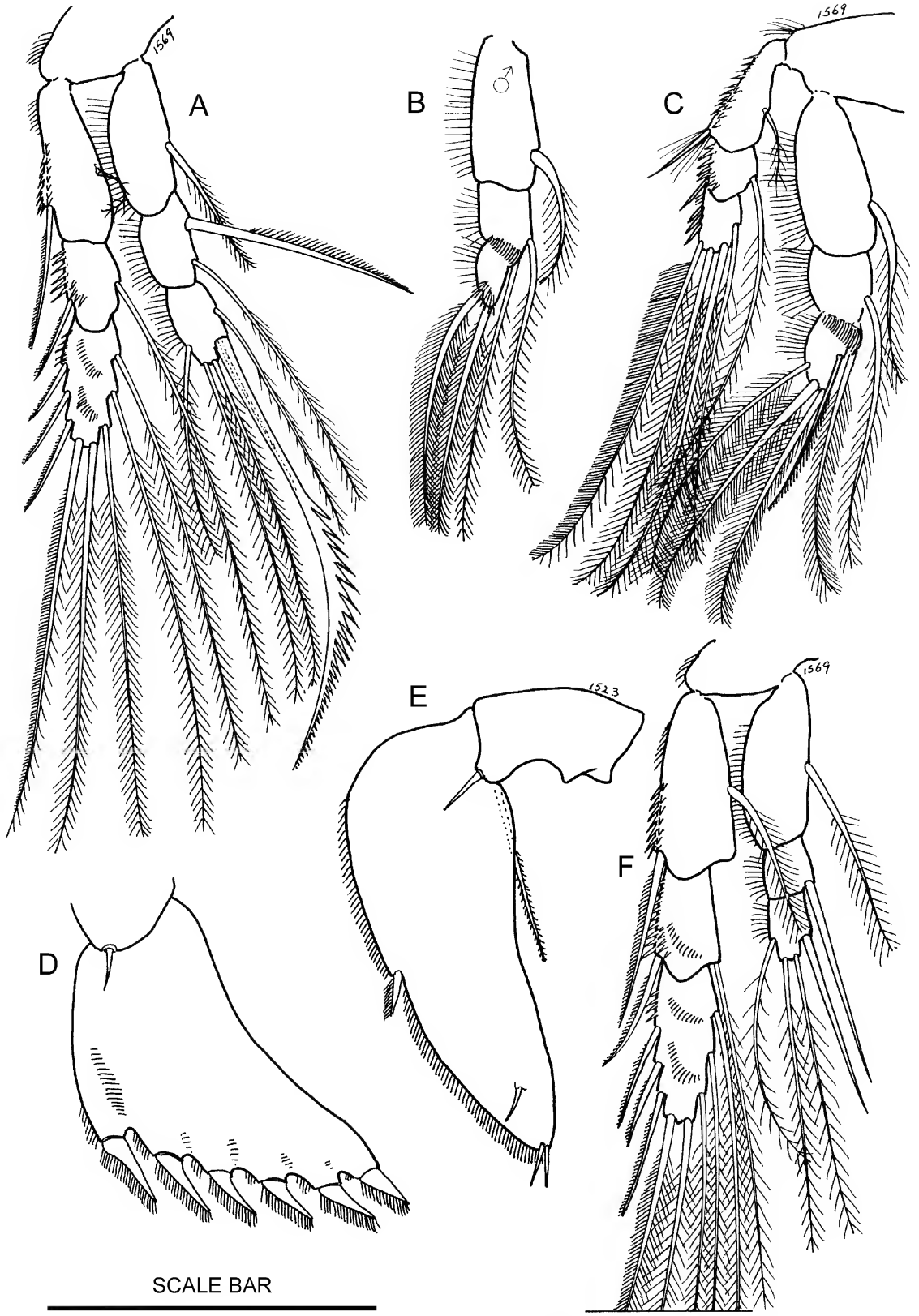

Figure 3. *Ravania wellsi* sp. nov. Female: A, P3. C, P2. E, P5 (dorsal). F, P4. Male: B, P2 endopod. D, P5 (ventral). Scale bar: A, D, E = 0.1 mm. B, C = 0.14 mm. F = 0.08 mm.

oval with keeled anterior half (Figs 4B, C). Dorsal pits and hyaline border as for female. Caudal rami quadrate, slightly longer than wide (Fig. 1C). Dorsal surface with network of ridges, medial edge straight with border setules distally, lateral edge convex with border setules distally. Terminal seta T1 unipinnate, recessed, T2 plain, almost as long as γ seta, T3 absent, T4 plain, set in from medial corner. Posterior border straight, fringed with fine setules. Antennule (Figs 2I, 4D)

characteristic of genus. Seta on segment 1 plumose, segment 3 with short, pointed spine-like denticle close to anterior lobe, δ seta very long (½ length of antennule), projects anteriorly (Fig. 2I), two tooth-like coupling denticles on segment 4, aesthetasc extremely long (almost as long as fully extended antennule (Fig. 2I), dactylus long, cylindrical. Endopod of P2 with two plumose terminal setae (Fig. 3B). No spinous setae on P4 endopod, all setae plumose. Dorsal surface of P5 exopod with pits, ventral setules at base of each terminal seta (Fig. 3D).

Etymology. The species has been named in recognition of Dr J. B. J. Wells' contribution to the taxonomy of the Harpacticoida.

Distribution. Type series collected from *Eucheuma denticulatum,* Point Vernon, Hervey Bay, PV4. 7/98, 41 ♀♀ (21 with eggs), 26 ♂♂, 14 juveniles. Also found on *Zonaria* sp., PV8, 8/00, 12 ♀♀, 14 ♂♂ at the same location. The species has been recorded at Arrawarra headland, northern NSW, on *Caulerpa vesiculosus* and *Dilophus* sp. V. A. Harris, 1982, 2000.

Ravania doliocauda sp. nov.

Figs 4–8, Plate 1E

Type material. HOLOTYPE adult male, length 0.66 mm, P81195; ALLOTYPE adult female, length 0.75 mm, P81196; PARATYPE specimens, 10 ♀♀, 6 ♂♂, P81197, deposited at AM, Sydney. Additional paratypes deposited at NHM, London. All collected from *Zostera capricornia* at Pulgul Creek mud flats, Urangan, Hervey Bay, Queensland (25°17'S 152°52'E), V. A. Harris, 30 Nov. 2002.

Diagnosis. Large denticle with serrated crown at base of δ seta on segment 3 of male antennule; female genital double-somite narrow (< ½ cephalosome width), no indication of division into anterior and posterior lobes, narrows to a point posteriorly, border setules absent except for a few at posterior apex, caudal rami excluded from posterior arch of genital double-somite; caudal furca dolioid (barrel-shaped in outline), rami long (l/w > 2), taper posteriorly, lateral and posterior edge convex, T1 lateral (½ way down ramus), γ seta recessed at posterolateral corner; medial patch of setules on labrum; male P2 endopod with three terminal setae.

Biometric data. *Females* (N = 32): maximum length (L_{max}) mean 0.75 mm, range 0.72–0.78 mm, body length (L_{urs}) mean 0.65 mm, range 0.62–0.69 mm; cephalosome width (W) mean 0.45 mm; rostrum width (R) 0.10 mm; genital double-somite length 0.135 mm, width 0.23 mm, arch 0.03 mm; caudal ramus length 0.13 mm, maximum width 0.06 mm (⅓ down ramus).

Ratios: L_{urs}/W 1.44; W/R 4.5–4.75; genital double-somite width 50% of body width, arch 22% of length; caudal ramus 20% of L_{urs}, ramus l/w 2.16, terminal seta T1 located 54% down lateral edge of ramus, Hicks' index for α 85%, for β 70%.

Males (N = 20): maximum length (L_{max}) mean 0.66 mm, range 0.62–0.67 mm; cephalosome width (W) mean 0.44 mm; rostrum length 0.055 mm (ventral); caudal ramus length 0.05 mm, width 0.05 mm; antennule length fully extended 0.165 mm; spermatophore 0.22 × 0.09 mm.

Ratios: L_{max}/W 1.5; caudal ramus 7.5% of L_{max}, ramus l/w 1.0; antennule 20% of L_{max}, antennule segment 2 24%, segment 3+4 36%, dactylus 24% of antennule length; spermatophore 33% of body length L_{max}.

Description. *Adult females* (Fig. 5A; Plate 1E, p. 163): colourless or very pale yellow (but see remarks below), outline of body oval, cephalosome semicircular with prominent rostrum, dorsal pits inconspicuous, very few dorsal sensilla mostly towards edge of cephalosome. Hyaline border clear, 7 μm wide (Fig. 5F). Labrum with central patch of very short setules (Fig. 6J). Genital double-somite (Fig. 5B, C) narrow, no epipleural expansion or division into anterior and posterior lobes, posterior half narrow (equals width of caudal rami), very fine filiform setules towards acutely pointed posterior, dorsal surface with transverse rows of shallow pits, no cleft, notch or scar to indicate boundary between anterior and posterior regions. Caudal arch shallow, encloses most of the anal segment, but caudal rami are excluded from arch. Female genital opening (Fig. 5D, E). Caudal furca dolioid (barrel-shaped in outline) (Fig. 5B). Each ramus narrows posteriorly, maximum width at level of β seta, lateral edge convex with border setules, medial edge without setules, posterior edge slightly convex, dorsal surface with pits and reticulate marking posteriorly (Fig. 6I).Terminal seta T1 halfway down lateral edge, γ seta recessed, T4 set in from medial corner. T3 absent. Antennule with pinnate seta on segment 1. Structure and setation of mouthparts and ambulatory limbs typical of family. Basis of antenna with row of small triangular setules (Fig. 6D), segment 2 of endopod with two lateral setae, geniculate setae with plain end segment, claw with fine comb-like edge. Mandible (Fig. 6H), maxillule (Fig. 6A), maxilla (Fig. 6C) and maxilliped (Fig. 6B). Segment 1 of P1 exopod (Fig. 6G) with crescent of fine setules parallel to edge, no area of denticulate setules on endopod. Spinous seta on P2 endopod segment 3 more than ½ endopod length (0.6:1) (Fig. 7C). Serrate spinous seta on segment 2 of P3 endopod almost as long as endopod (Fig. 7B), large serrate spinous seta on segment 3 longer than endopod (1.4:1). P4 endopod with internal spinous seta on segment 2 and first (internal) spinous seta on segment 3 plain (Fig. 7E). Baseoendopod of P5 with long ventral seta (½ length of exopod), exopod broad (l/w = 1.67), ovate with acute apex (Fig. 6E), strong ventral falciform ridge, long border setules, one subterminal dorsal seta and two apical setae (Fig. 6F), P5s extend back ¾ length of caudal rami and compensate for the narrow genital double-somite by forming most of the roof to the brood chamber. Females carry 10 eggs per brood.

Adult males (Fig. 8A; Plate 1F, p. 163). Colourless or very pale yellow. Outline of body oval, anterior of cephalosome semicircular (not truncated), rostrum keeled, oval in ventral view (Fig. 8C). Dorsal pits, sensilla and hyaline border as for female. Caudal ramus (Fig. 8E) quadrate, setation similar to female T1 lateral, T3 absent, T4 at medial corner. Antennule (Fig. 7F) with pinnate seta on segment 1, δ seta on segment 3 long (equal to segment 3+4+ dactylus in length), points forward, coupling denticle on segment 3 large with serrated crown, two tooth-like denticles on segment 4 (Fig. 8F), dactylus ⅔ length of segment 3+4, apex pointed (Fig. 8G). Other limbs as for female except P2 (Fig. 7D) has three terminal setae on endopod (two plumose, one serrulate spinous). P5 acutely trapezoidal, first (lateral) seta of different shape to terminal setae (Fig. 8D), first row of ventral setules about 16, row of four or five setules at base

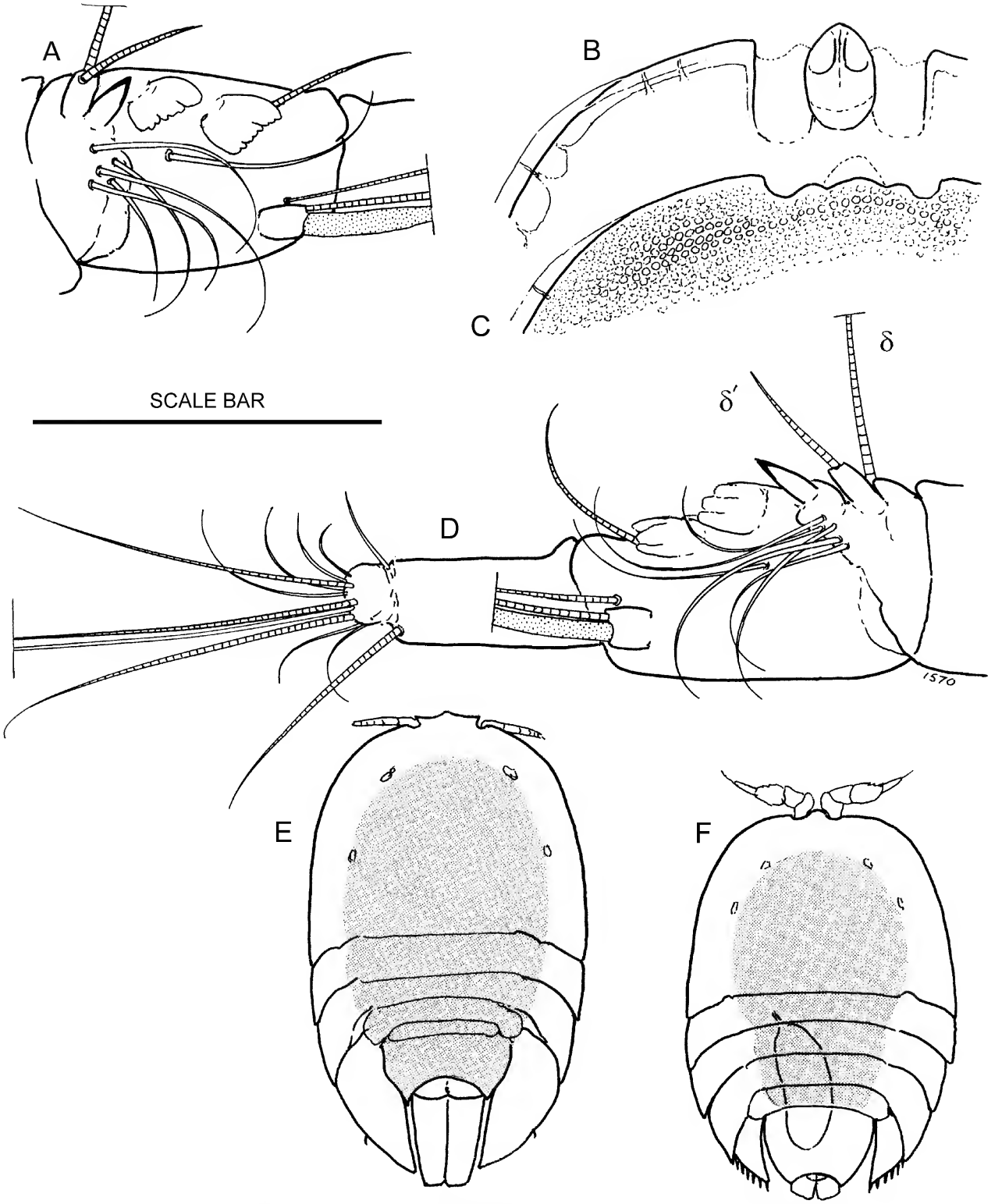

Figure 4. *Ravania wellsi* sp. nov. Male: *(A)* antennule coupling denticles; *(B, C)* anterior cephalosome (ventral, dorsal); *(D)* antennule (detail of dactylus). *Ravania doliocauda* sp. nov. coloured variety from Cairns, northern Queensland: *(E)* adult female; *(F)* adult male. Scale bar: A, D = 0.04 mm. B, C = 0.15 mm. E, F = 0.58 mm.

of each terminal seta. Spermatophore relatively large (⅓ body length).

Etymology. The specific name refers to the outline of the caudal furca (L. *doliolum* = a small barrel or cask + *cauda* = tail).

Remarks. All specimens collected at low tide from seagrass on the Pulgul Creek mudflats at the Urangan collection site are heavily contaminated with silt particles plus a wide variety of attached organisms (bacteria, protozoa, moulds, unicellular algae, diatoms, filamentous algae etc.). This makes critical observation of fine structure difficult or

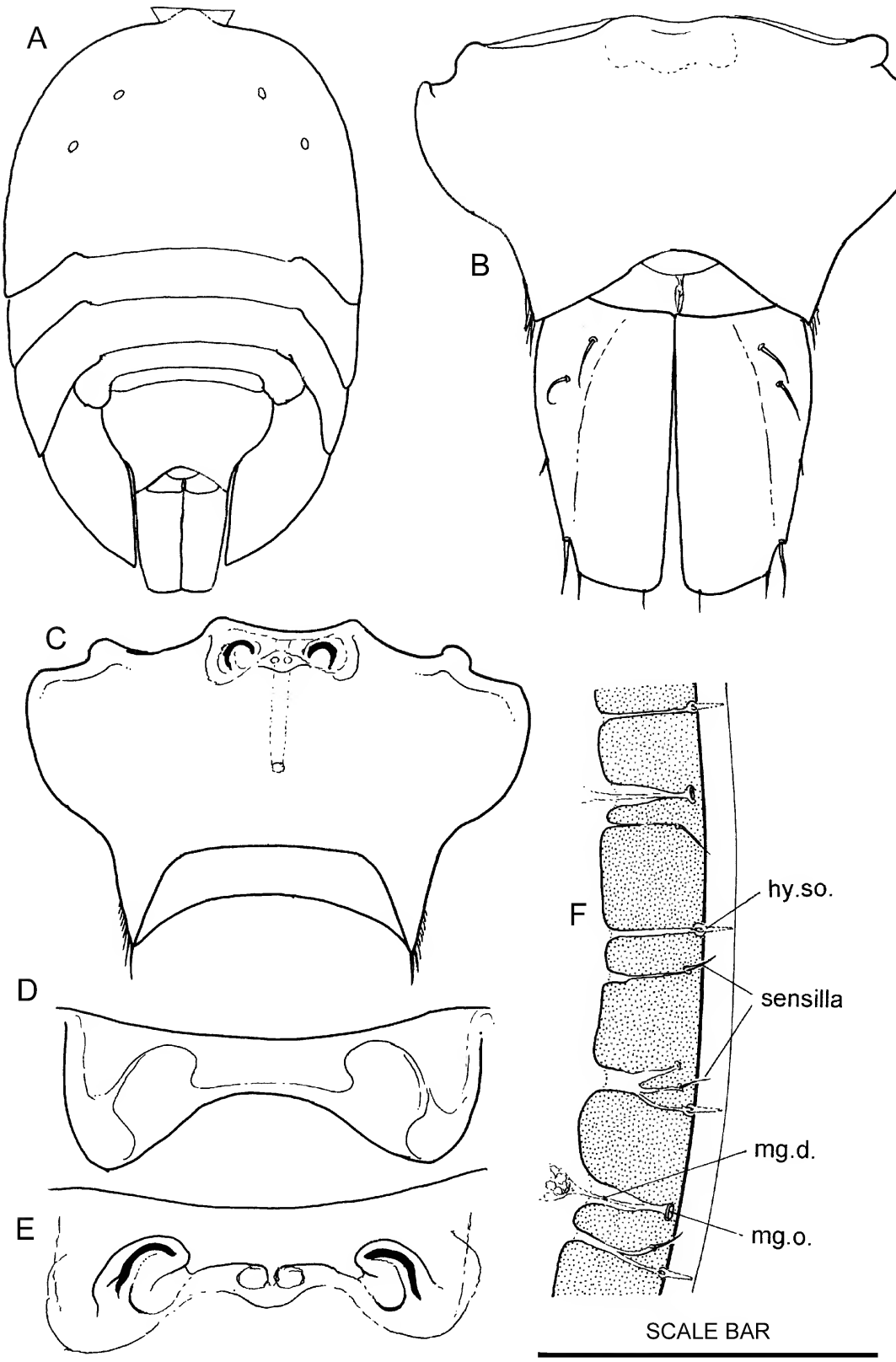

Figure 5. *Ravania doliocauda* sp. nov. Female: *(A)* adult; *(B)* genital double-somite and caudal rami; *(C)* genital double-somite (ventral); *(D, E)* Genital opening (superficial and deep focus); *(F)* cephalosome border (*hy.so.* hyaline border sense organ; *mg.d.* marginal gland duct; *mg.o.* opening to marginal gland). Scale bar: A = 0.45 mm. B, C = 0.15 mm. D, E = 0.06 mm. F = 0.08 mm.

impossible. Various methods using detergents, enzymes and ultrasonic vibration have been used with varying success to clean the animals before dissection, but such treatment often destroys the fine structure of setae and setules.

Apart from their tolerance to a muddy environment, this species can survive wide environmental temperature and

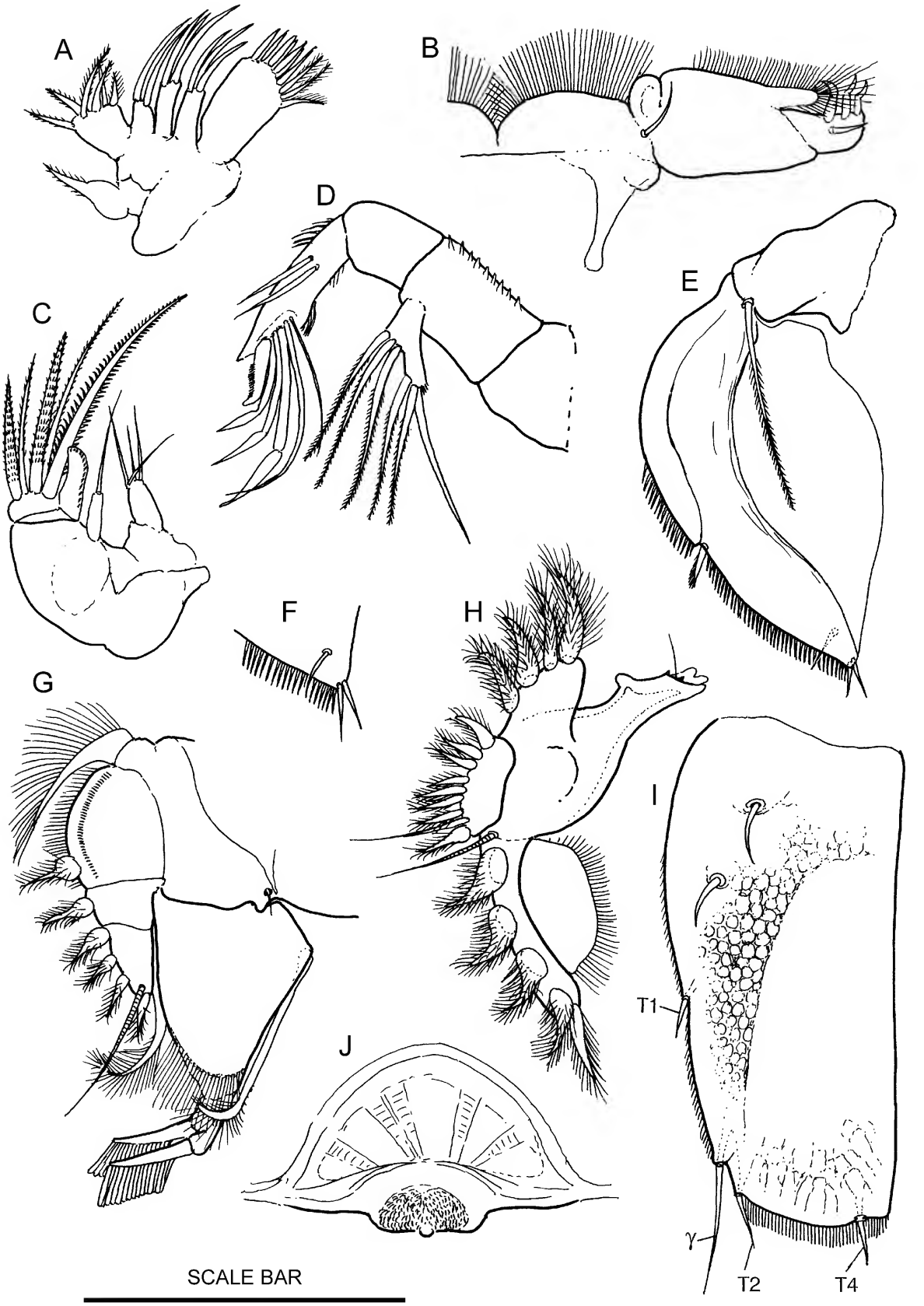

Figure 6. *Ravania doliocauda* sp. nov. Female: *(A)* maxillule; *(B)* maxilliped; *(C)* maxilla; *(D)* antenna; *(E)* P5 (ventral); *(F)* apex of P5; *(G)* P1; *(H)* mandible; *(I)* caudal ramus (dorsal); (J) labrum. Scale bar: A, C = 0.08 mm. B, D, H, I, J = 0.1 mm. E = 0.19 mm. G = 0.14 mm.

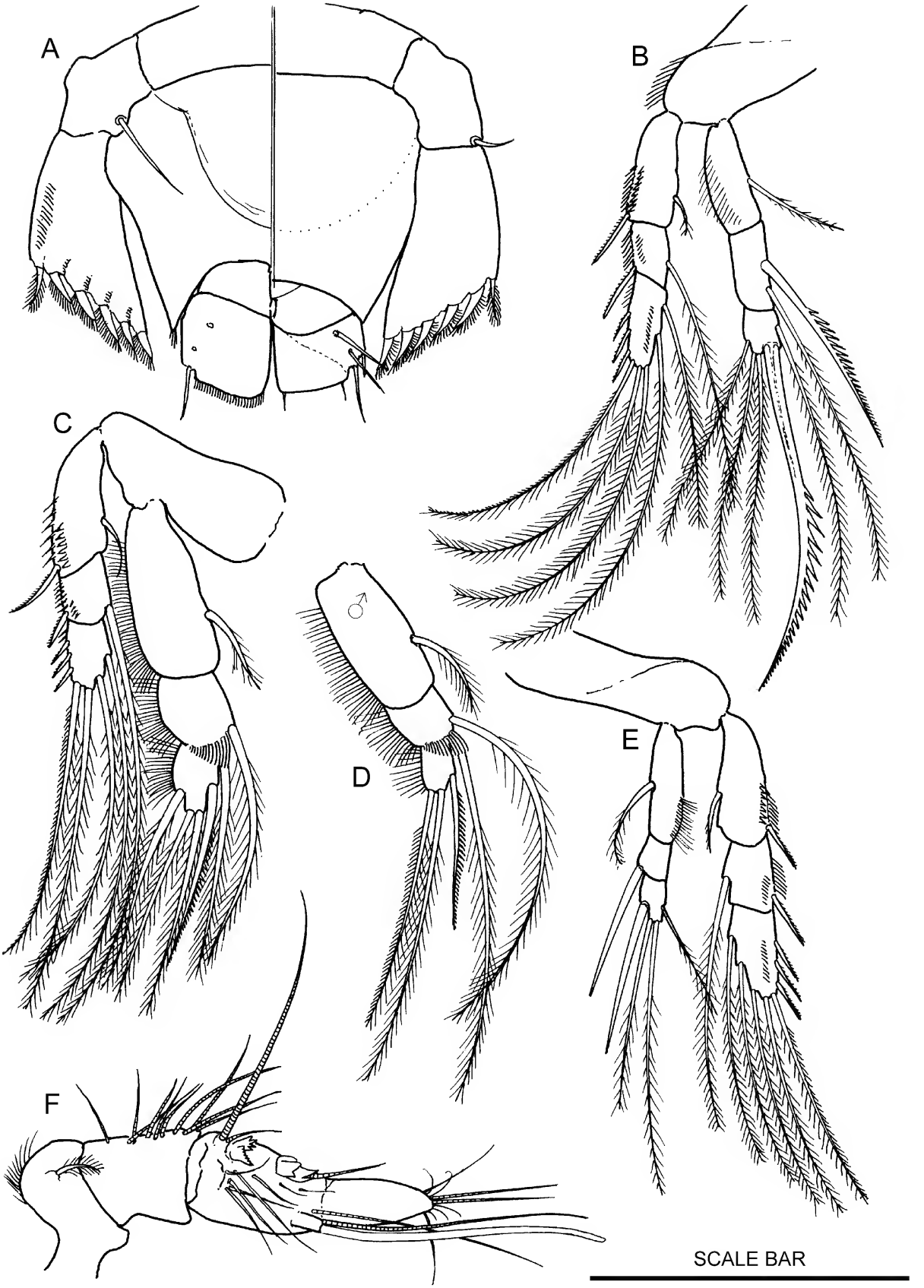

Figure 7. *Ravania doliocauda* sp. nov. Male: *(A)* genital somite, P5 and caudal rami (ventral, dorsal); *(D)* P2 endopod; *(F)* antennule. Female: *(B)* P3; *(C)* P2; *(E)* P4. Scale bar: A, C, D, E = 0.14 mm. B = 0.19 mm. F = 0.1 mm.

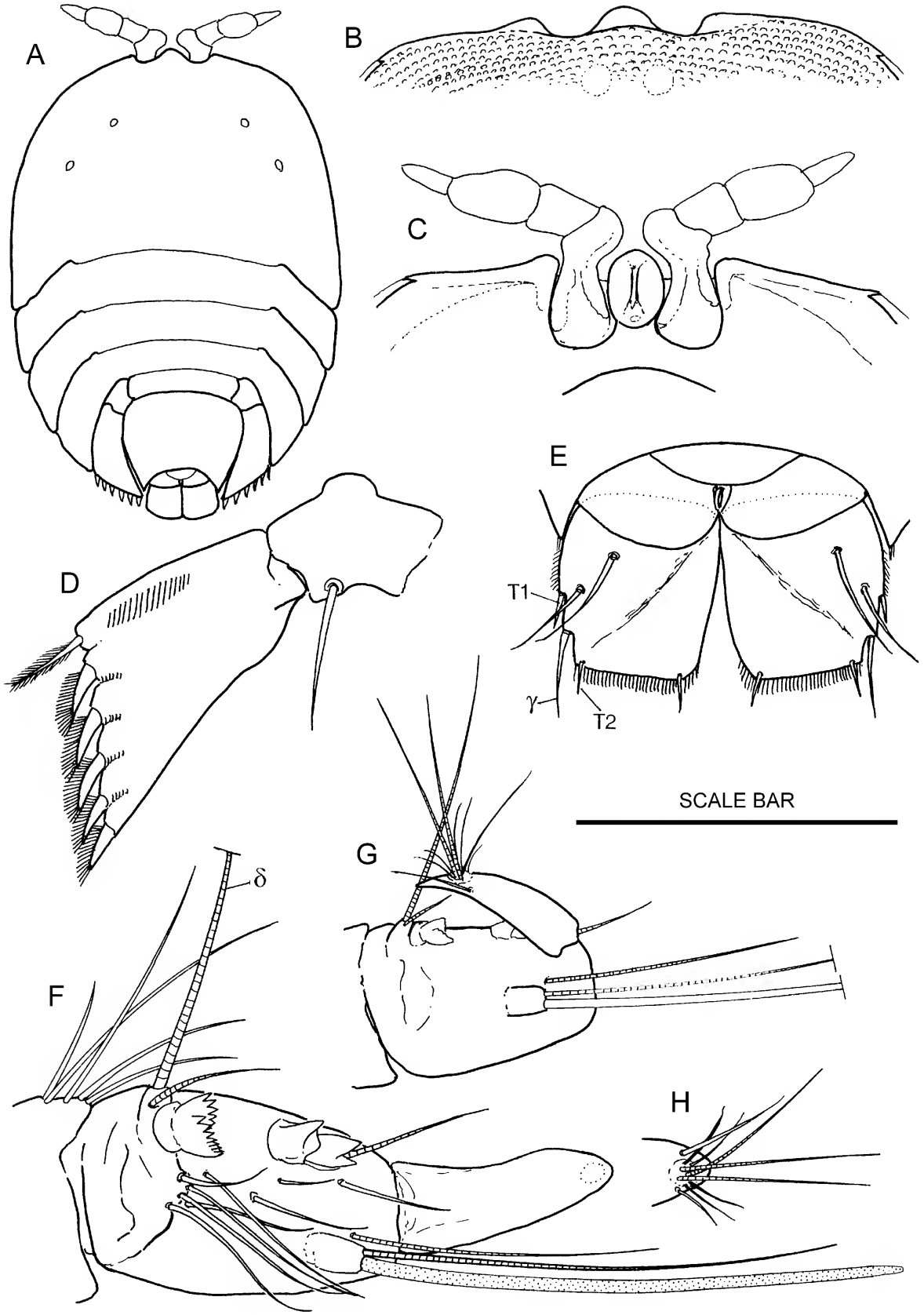

Figure 8. *Ravania doliocauda* sp. nov. Male: *(A)* adult; *(B, C)* anterior of cephalosome (dorsal, ventral showing rostrum); *(D)* P5 (ventral); *(E)* caudal rami; *(F)* antennule showing coupling denticles; *(G, H)* dactylus of antennule. Scale bar: A = 0.45 mm. B, C = 0.23 mm. D = 0.11 mm. E = 0.1 mm. F = 0.06 mm. G = 0.08 mm.

salinity changes. Low water during spring tides tend to occur about midday or early afternoon at Urangan leaving the seagrass beds exposed to solar radiation for up to three hours. On 30 November 2002 at 12.30 pm when the type population sample was collected, water temperature in very shallow pools containing seagrass was recorded at 31°C, despite the fact that the weather was overcast with showers. Heavy rain occurring during the low tide period, particularly during the cyclone season, will flood the mud flats and subjects all organisms living there to lowered salinity or fresh water.

Distribution. The type series (PCk 3. 11/02) was collected from *Zostera capricornia* on mud flats at low water spring tide. It comprised 147 ♀♀ (91 carrying eggs), 122 ♂♂ and 26 copepodids. This species has been collected from another seagrass *Cymodocea serrulata* in the same area, (PCk 1. 4/97. 116 ♀♀ (67 with eggs), 108 ♂♂ and 21 copepodids), but it has not been found on two other seagrasses, *Halophila ovalis* and *H. spinulosa*, both abundant in the same area, V. A. Harris 1997, 2002. A coloured form of *R. doliocauda* with large red area on back (Fig. 4E, F) was collected from sea grass (? *Zostera capricornia*) growing on coral sand in shallow water inside the coral reef at Green Island, Cairns, Queensland (16°43'S 146°E) 4 ♀♀, 2 ♂♂, V. A. Harris 1973.

Genus *Synurus* gen. nov.

Porcellidium.—Ummerkutty, 1970: 158.

Type species. *Synurus ctenocheirus* sp. nov.

Diagnosis. Male genital double-somite fused to metasome segment 4 and baseoendopod of P5; epipleural lobe of male metasome segment 3 long, stretches back to posterior extremity of caudal ramus; male P5 exopod ovate (not trapezoidal) with one lateral seta, terminal setae atrophied or absent; seta T1 absent from male and female caudal ramus; segment 3 of P2, P3 and P4 exopod with only two external setae; anterior of male cephalosome deeply concave; anterior of female cephalosome truncated; female P5 exopod without ventral expansion, P5s reach beyond genital double-somite but do not touch posteriorly; spermatophore elongate, ephemeral on female.

Species composition. *Synurus unicus* (Ummerkutty, 1970) comb. nov.; *S. ctenocheirus* sp. nov.

The genus is known from Gulf of Mannar, Sri Lanka (Ceylon), Okinawa, Japan and the Great Barrier Reef, Australia.

Etymology. The name *Synurus* (masculine) refers to the fusion of the anal segment with the caudal rami on female specimens of the type species (G. *syn* = together, conjoint + *oura* = tail).

Remarks. Males of this genus are unique among the Porcellidiidae in having an ovate P5 exopod with long lateral seta and terminal setae that are atrophied or absent. This limb strongly resembles the general form of the female P5, except for the absence of a ventral falciform ridge and dorsal setae.

Synurus ctenocheirus sp. nov.

Figs 9–12, Plate 1G, H

Type material. HOLOTYPE adult male, length 0.55 mm, P81213; ALLOTYPE adult female, length 0.68 mm, P81214; PARATYPE specimens, 6 ♀♀, 4 ♂♂, P81215, deposited at AM, Sydney. Additional paratypes deposited at NHM, London. All washed from seagrass *Zostera* sp., collected at Green Island, Cairns, Queensland, Australia (16°41'S 145°56'E), V. A. Harris, 1973.

Diagnosis. First (proximal) claw on P1 endopod ctenoid (comb-like) with recurrent teeth, second claw lamelliform; female caudal ramus fused to anal segment; male antenna with seta on basis (absent from females, Fig. 10A); male P5 exopod with long lateral seta, terminal setae absent except for two small spine-like atrophied setae; female rostrum extremely broad (⅓ cephalosome width).

Biometric data. *Females* (N = 10): maximum length (L_{max}) mean 0.68 mm, range 0.67–0.70 mm, body length (L_{urs}) mean 0.66 mm, range 0.65–0.68 mm; cephalosome width 0.44 mm, range 0.43–0.45 mm; rostrum 0.14 mm; genital double-somite width 0.18 mm, length 0.2 mm, arch 0.08 mm; caudal ramus length 0.078 mm, width 0.022 mm [length of caudal ramus from point of fusion with the anal segment (indicated by a slight notch, see Fig. 9)].

Ratios: L_{urs}/W 1.5; W/R 3.0, cephalosome length 60% of L_{max}; genital double-somite w/l 0.9, height of arch 40% of length; caudal ramus l/w 3.8, 12% of L_{urs}, Hicks' index for β 60%, distance between α and β setae 25% of ramus length.

Males (N = 10): maximum length (measured from anterior edge of shoulder L_{max}) mean 0.55 mm, body length (from rostrum L_{urs}) mean 0.48 mm, range 0.47–0.50 mm; cephalosome width 0.37 mm; caudal ramus length 0.047 mm, width 0.028; antennule length (fully extended) 0.10 mm; spermatophore 0.09 × 0.02 mm.

Ratios: L_{urs}/W 1.3, L_{max}/W 1.5; cephalosome length 67% of L_{max}; caudal ramus l/w 1.7; antennule 18% of body length (L_{urs}), antennule segments 3+4 57% and dactylus 18% of antennule length; spermatophore 18% of body length (L_{urs}).

Description. *Adult females* (Fig. 9A; Plate 1G, p. 163): colour lemon yellow. Body outline an ellipse (e = 0.814) strongly truncated anteriorly with slight bulge in midline. Cephalosome length greater than half maximum length of animal. Rostrum very wide (⅓ body width). Dorsal pits inconspicuous (1–1.5 µm), a few dorsal sensilla present. Hyaline border clear, 7 µm wide (Fig. 9D), surrounds cephalosome, ducts of marginal glands open dorsally. Genital double-somite cordate (Fig. 9B), length greater than width, no notch or scar to indicate boundary between anterior and posterior lobes, no anterolateral ridges (rugosities), border setules very small, posterior extremity pointed, terminated by four or five small setules. Posterior arch deep, nearly all of rami enclosed in arch. Caudal ramus long, narrow, rhomboid with parallel sides (Fig. 9F), fused to anal segment. Dorsal surface with very small dorsal pits (< 1 µm) and parabolic ridge on each ramus that fits the edge of genital double-somite arch. Seta T1 absent, γ seta at lateral corner, posterior border oblique, T4 at rounded apex, T2 and T3 very close mid-way along oblique edge (they tend to lie parallel to edge), terminal fringe of very fine setules between T3 and T4 (Fig.

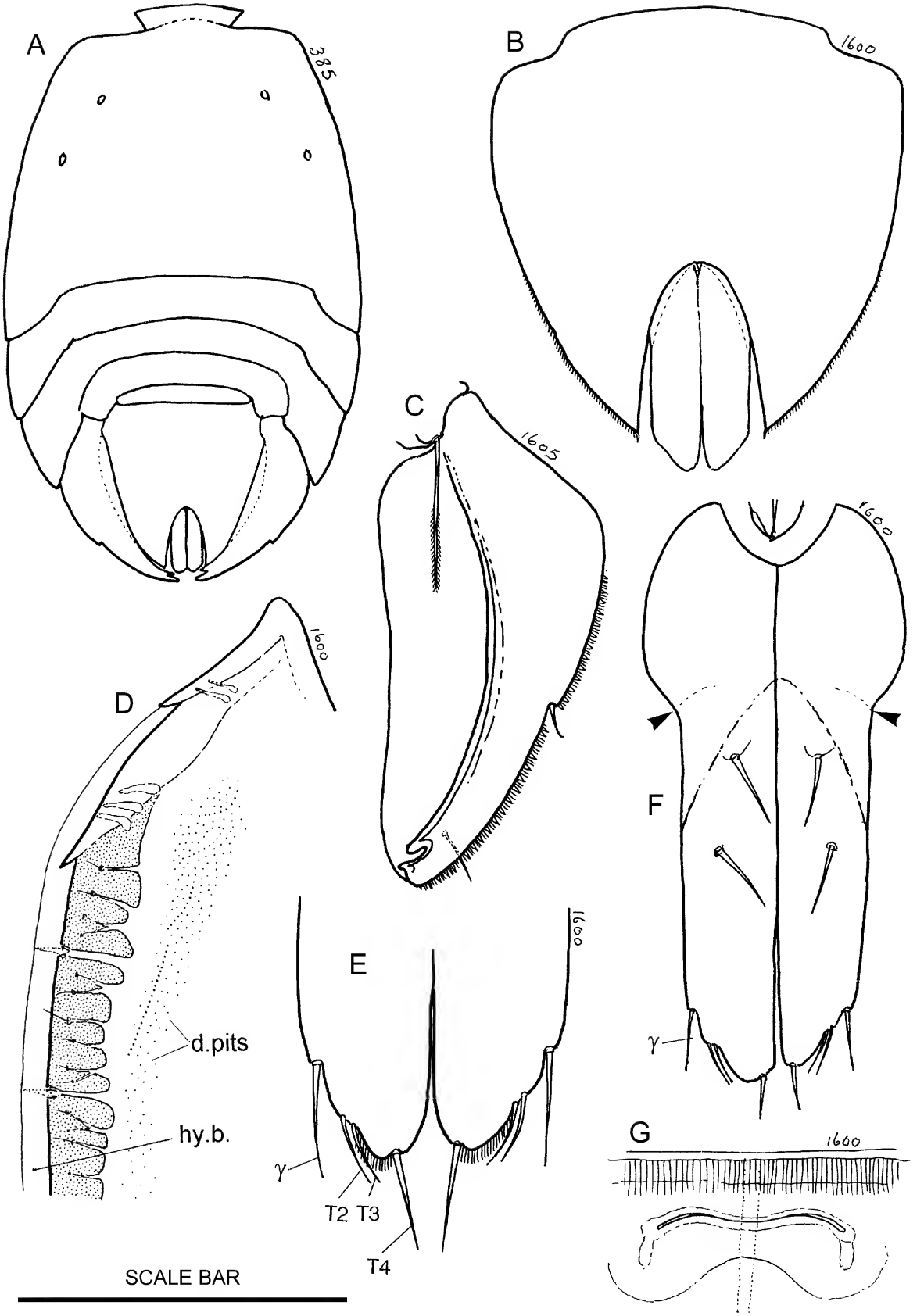

Figure 9. *Synurus ctenocheirus* sp. nov. Female: *(A)* adult; *(B)* genital double-somite; *(C)* P5 (ventral); *(D)* edge of cephalosome (*d. pits*, dorsal pits; *hy.b.* hyaline border); *(E)* detail of terminal setae on caudal rami; *(F)* caudal rami showing fusion of anal segments with rami (arrow marks point of fusion); *(G)* genital opening. Scale bar: A = 0.45 mm. B, C = 0.15 mm. D, F = 0.08 mm. E = 0.06 mm. G = 0.12 mm.

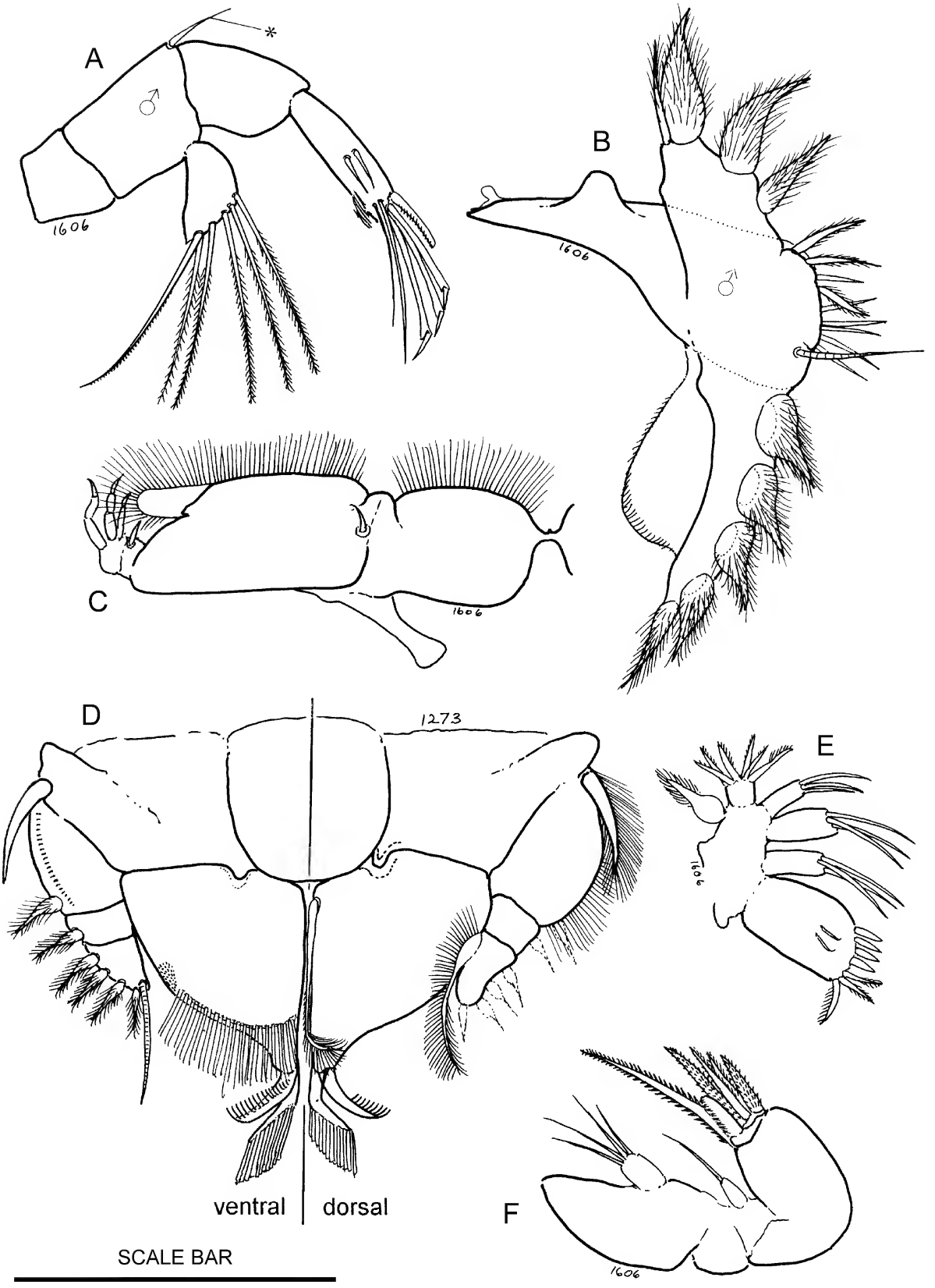

Figure 10. *Synurus ctenocheirus* sp. nov. Male: *(A)* antenna (* seta on basis); *(B)* mandible. Female: *(C)* maxilliped; *(D)* P1; *(E)* maxillule; *(F)* maxilla. Scale bar: A = 0.1 mm. B, C, E, F = 0.08 mm. D = 0.14 mm.

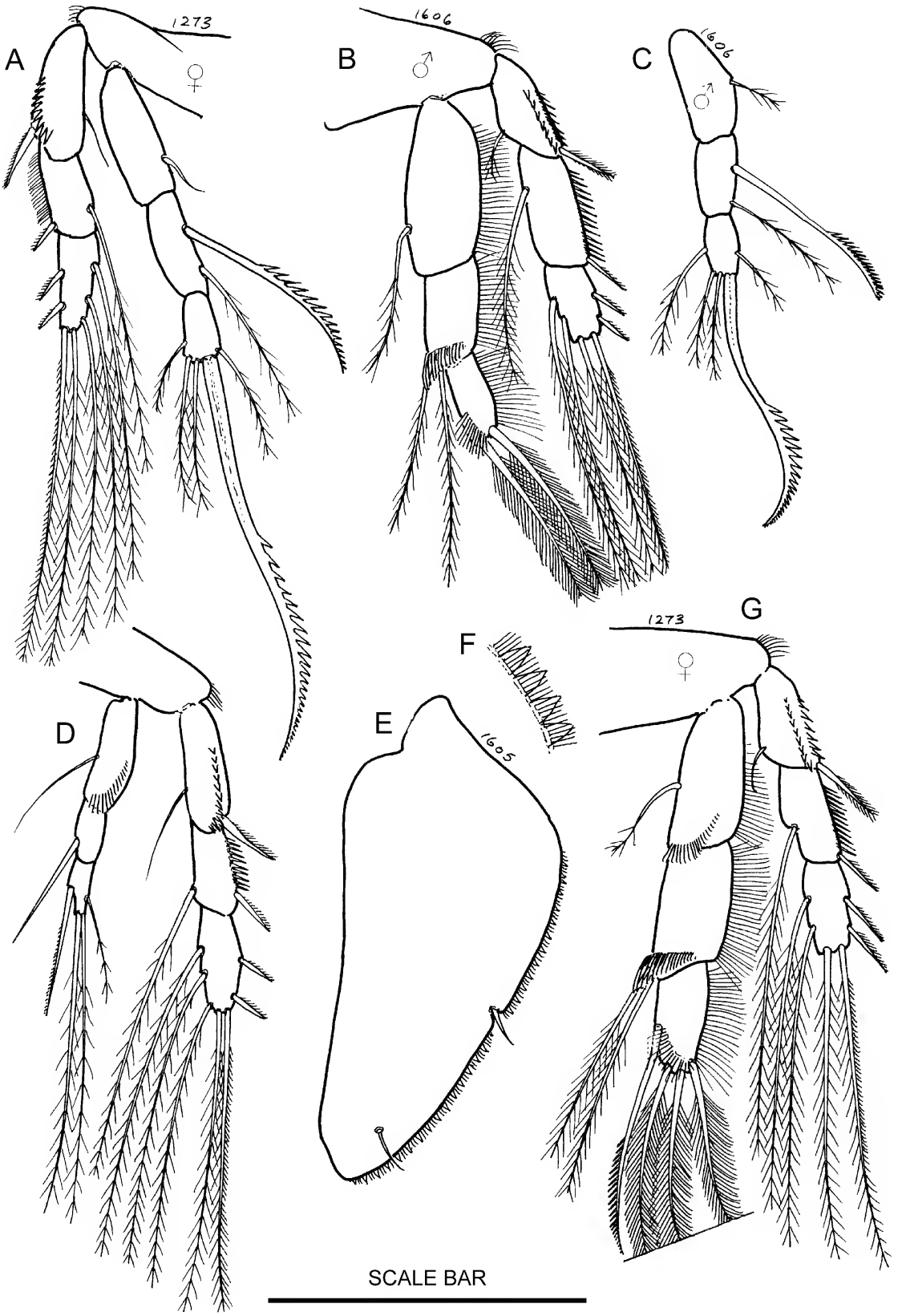

Figure 11. *Synurus ctenocheirus* sp. nov. Female: *(A)* P3; *(D)* P4; *(E)* P5 (dorsal); *(F)* border setules of P5; *(G)* P2. Male: *(B)* P2; *(C)* P3 endopod. Scale bar: A, C, D, G = 0.14 mm. B = 0.1 mm. E = 0.17 mm.

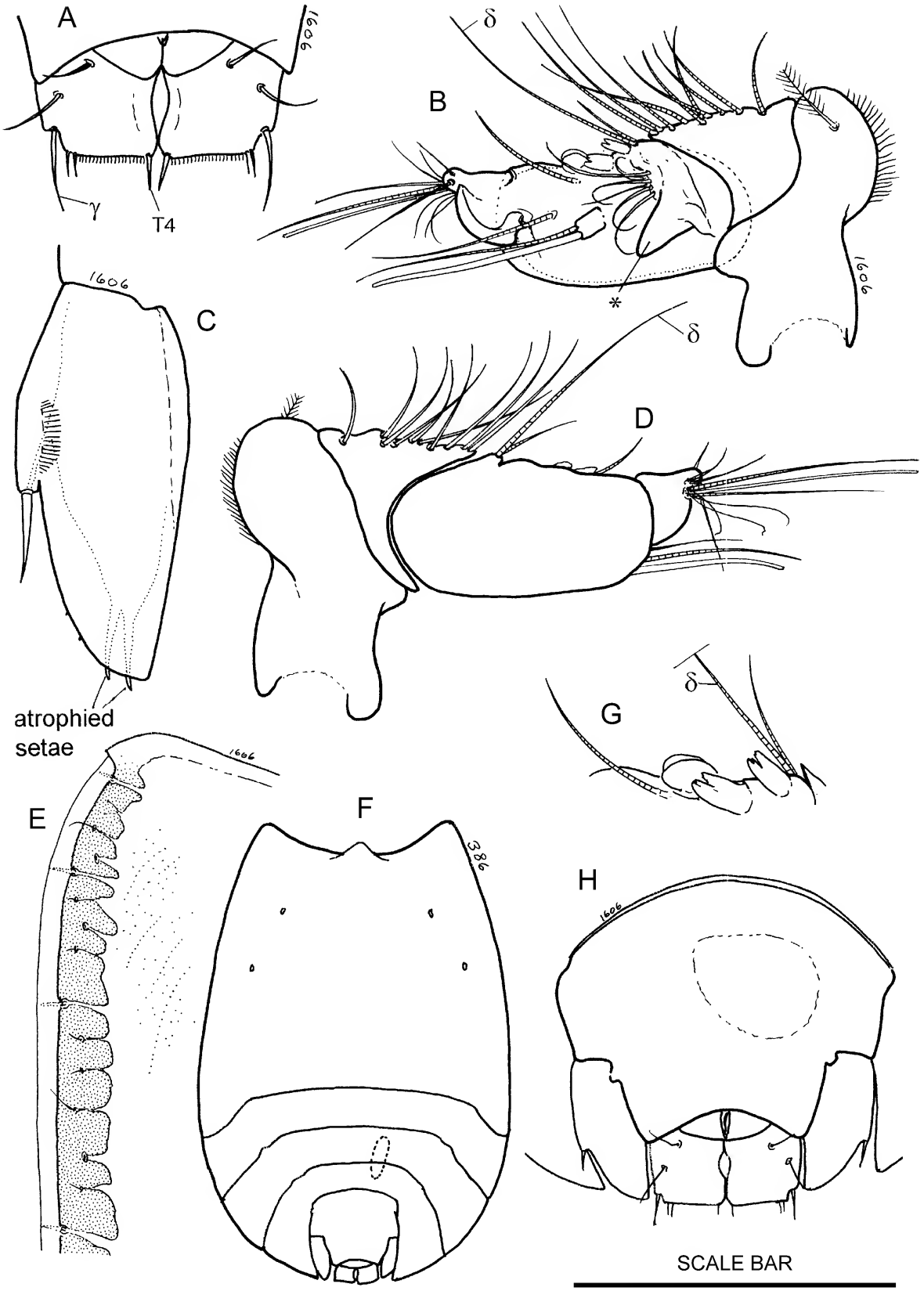

Figure 12. *Synurus ctenocheirus* sp. nov. Male: *(A)* caudal rami; *(B)* antennule, ventral (* ventral process); *(C)* P5 (ventral); *(D)* antennule, dorsal; *(E)* edge of cephalosome; *(F)* adult with spermatophore; *(G)* coupling denticles on antennule; *(H)* genital double-somite and caudal rami (showing fusion of genital double-somite with metasome segment 4 and P5 baseoendopod. Scale bar: A, B, D, E, H = 0.08 mm. C = 0.06 mm. F = 0.45 mm. G not to scale.

9E). Structure and setation of mouthparts and ambulatory limbs typical of family except that segment 3 of P2, P3 and P4 exopod has only two spine-like external setae (Figs 11A, B, D, G). Antenna basis without seta (cf. male), exopod with five plumulose setae and one finely serrulate spine-like seta, geniculate setae on endopod with plain terminal segment, terminal claw with fine comb (Fig. 10A). Mandible (Fig. 10B), maxillule endopod with six setae (Fig. 10E), maxilla (Fig. 10F), coxae of maxillipeds touch in midline, basis with fimbriate process (Fig. 10C). First segment of P1 exopod with crescent of denticulate setules (Fig. 10D, left side), first segment of endopod broad (l/w = 1.1), area of denticulate setules at lateral end of fimbriate crescent, first claw on terminal segment comb-like with recurved teeth, second claw lamelliform (Fig. 10D). Serrulate spinous seta on segment 3 of P2 endopod more than ½ length of endopod (0.6:1, Fig. 11G). Serrate spinous seta on segment 2 of P3 endopod ⅔ length of endopod (Fig. 11A), large serrate spinous seta on segment 3 longer than endopod (1.38:1). P4 (Fig. 11D) seta on endopod segment 2 and first internal seta of segment 3 plain spinous. P5 exopod (Fig. 9C, 11E) broad, lanceolate with blunt apex, ventral falciform ridge terminates in a deep indentation or notch that appears to fit round the end of the caudal ramus on some specimens (Fig. 9C), medial edge of P5's dorsal expansion overlaps genital double-somite extensively, ventral expansion absent, only one sub-terminal dorsal seta present, dorsal pits absent from P5, lateral border with double row of setules (ventral row of triangular setules and dorsal row of short filiform setules (Fig. 11F). Females carry four large eggs.

Adult males (Fig. 12F; Plate 1H, p. 163). Colour lemon yellow. Outline of cephalosome a truncated hemi-ellipse, deeply concave anteriorly with small medial bulge. Cephalosome unusually long (⅔ body length). Posterior region of body (metasome plus genital double-somite with P5s) semicircular. Epipleural lobes of third metasome segments very long, they wrap round P5s plus caudal rami and extend back as far as the posterior limit of the body (Fig. 12F, H). Rostrum not keeled ventrally, dorsal pits and hyaline border (Fig. 12E) as for female. Caudal rami (Fig. 12A) not fused to anal segment, more or less rectangular, medial edge concave leaving an opening between the rami, lateral edge slightly convex, posterior border straight. T1 absent, γ seta recessed at lateral corner, T2 and T3 small, very close together, T4 at medial corner, fringe of short setules along posterior border between T3 and T4. Limbs as described for female except for the following differences. First segment of antennule with pinnate seta (Fig. 12B), second segment short, very narrow posteriorly (Fig. 12D), segment 3+4 unusually long (> ½ total length of antennule), ventral process or blade present, two small tooth-like and one rounded coupling denticle present on segment 4 (Fig. 12G), no denticulate pad or brush-pad present, aesthetasc and σ seta short (about length of segment 3+4), dactylus broad, very short (¼ length of segment 3+4). Antenna with seta at distal end of basis (Fig. 10A, (absent in female). P1 as for female, P2 with two plumose terminal setae on endopod (Fig. 11B), P3 similar to female but terminal serrate seta on endopod is S-shaped and equal to length of endopod (Fig. 11C). P5 baseoendopod fused with metasome segment 4 and genital double-somite. Exopod of P5 appears to articulate with fused genital somite (Fig. 12H), exopod ovate with one plain lateral seta half way down lateral edge (Fig. 12C) and row of 15+ ventral setules, two microscopic spinules (representing atrophied terminal setae) near apex (Fig. 12C). Spermatophore very small (Fig. 12F).

Etymology. *Synurus ctenocheirus* has been named from the unique condition of the first terminal comb-like seta on P1 endopod. In all other members of the Porcellidiidae both claws are lamelliform, Harris and Robertson (1994), but in adult and late stage copepodids of this species the first claw is comb-like (G. *ctenos* = a comb + *cheiros* = hand).

Remarks. *Synurus ctenocheirus* is remarkable for four unique sexually dimorphic features: presence of a seta on basis of male antenna, epipleural lobes of male metasomal segment 3 that extend back to the same level as the P5 limbs, fusion of male M4 with genital double-somite and P5 baseoendopod, and fusion of female caudal rami with the anal segment.

Animals named *Porcellidium unicus* by Ummerkutty (1970), although not fully described, clearly belong to the genus *Synurus* by virtue of the oval male P5 with atrophied setae, only two external setae on P2, P3 and P4 exopod segment 3, and the fusion of male genital double-somite with P5 baseoendopod and M4, but these features exclude the species from *Porcellidium*. It should be renamed *Synurus unicus* (Ummerkutty, 1970) comb. nov.

The following characters distinguish *S. unicus* from *S. ctenocheirus*. It is larger (female 0.75 mm, male 0.63 mm), Hicks' index for β is 50%, the distance between α and β setae is ½ ramus length and the female caudal ramus is not fused to the anal segment. The male P5 is described as pentagonal bordered with setules on lateral edge as far as the lateral seta and there are three atrophied terminal setae. *Synurus unicus* was collected from algae off Vedalai in the Gulf of Mannar, Sri Lanka.

Distribution. The type series GI2,9/73 (comprising 44 ♀♀, 30 ♂♂ + 23 juveniles) was collected from *Zostera capricornia* growing on coral sand in the sublittoral fringe at Green Island, Great Barrier Reef, Cairns, but it has not been recorded from the southern coast of Queensland (25°S), V. A. Harris, 1973. Specimens of this species collected from Okinawa, Japan (approx. 27°N) in the collection of Yuka Sasaki have been examined by the author. They appear morphologically identical to the Australian material. Their size falls within the range given above (Yuka Sasaki, pers. comm.).

Genus *Kensakia* Harris & Iwasaki, 1997

Kensakia Harris & Iwasaki, 1997: 136.
Acutiramus.—Harris & Robertson, 1994: 289.
Porcellidium.—Thompson & Scott, 1903: 275; Kim & Kim, 1997: 153; Walker-Smith, 2001: 665; Wells, 2007: 79.

Type species. *Kensakia acuta* (Kim & Kim, 1997)

Diagnosis. Segment 3 of male antennule with triangular denticle at base of δ seta (not comb-like), segment 4 with large pad of hair-like setules (brush-pad) and small distal denticle; adult female genital double-somite cordate, caudal ramus trapezoid, terminal seta T1 present, T2 absent from female but present on male caudal ramus, T3 absent from both male and female; ventrolateral band of surface markings on underside of cephalosome; maxillule endopod with six setae; coxal lobes of maxillipeds touch in midline; spermatophore elongate, ephemeral on female.

Species composition. *Kensakia acuticaudata* (Thompson & Scott, 1903) comb. nov.; *Kensakia acuta* (Kim & Kim, 1997); *K. shimodensis* Harris & Iwasaki, 2009; *K. parva* Harris & Iwasaki, 2009; *K. australis* sp. nov.

The genus has a wide range. It is represented in Japanese and Korean waters, southern Gulf of Thailand, North East coast of Australia, Sri Lanka and the Suez Canal.

Etymology. The specific name refers to the pointed shape of the caudal rami (Japanese, *Kensaki* = point of a sword).

Remarks. The genus was first defined to accommodate a single species from Kadonohama Bay, Iwate Prefecture, Japan, Harris & Iwasaki (1997). Since then three closely related species have been collected from Japan, Malaya and Australia which share the same unique set of characters and justify admission to the genus.

The characteristic brush-pad of male *Kensakia* differs from the denticulate pad described for genera such as *Murramia* or *Porcelloides* because it is only attached to the antennule by its proximal edge. It is possible to lift it up as a flap (see Figs 13I). It is the most conspicuous apomorphic character defining the genus. Markings on the under surface of the cephalosome (see Fig. 13I, left figure) may form a band parallel to the hyaline border (ventrolateral band). It has been found on all species examined. This band is structurally different from the condition in *Tectacingulum* because it does not involve displacement of the hyaline membrane or its sensilla.

The diagnostic characters listed above clearly separate members of *Kensakia* from other superficially similar genera (i.e., *Ravania, Acutiramus* and *Porcelloides*).

Female specimens in the NHM collection labelled *Porcellidium acuticaudatum* Thompson & Scott 1903 (1928, 4,2,43), collected from Lake Timsâh, Ismalia, by the Cambridge University Expedition to the Suez Canal, Gurney (1924), were examined by the author. Females have a trapezoid caudal ramus, but T2 and T3 are missing which eliminates them from *Porcelloides*. They also have a distinct notch at the posterior end of the falciform ridge on P5 (compare with Fig. 14A). These are all characteristics of *Kensakia* and eliminate *P. acuticaudatum* from *Porcellidium*, *Acutiramus* and *Ravania*. Unfortunately, details of the male antennule, which would have confirmed that *P. acuticaudatum* belongs to *Kensakia*, could not be resolved on the specimen examined, however the male cephalosome is only slightly truncated with broadly rounded shoulders as in *K. australis*. Illustration of the male by Gurney (1927) lacks important detail, but P5 is shown trapezoid and P2 has two terminal setae on endopod. This suggests that the species should be renamed *Kensakia acuticaudata* (Thompson & Scott, 1903) comb. nov.Thompson & Scott found three female specimens in washings from Muttuvaratu pearl oysters, Sri Lanka (formerly Ceylon), but material from Ismalia was washed from *Sargassum* sp., and *Halophila* sp., Gurney (1927). The species is described as "…vivid rosy red or red spots on thorax and abdomen", Gurney (1927).

Key to species of *Kensakia*

Kensakia acuticaudata (Thompson & Scott, 1903) has not been included in this key due to lack of data on male characters.

1 Numerous dorsal sensilla on cephalosome (>200). Distal coupling denticle on segment 4 of male antennule relatively large (10–15 µm) ..... *Kensakia shimodensis* Harris & Iwasaki, 2009

—— Dorsal sensilla not numerous (< 50). Distal coupling denticle on segment 4 of male antennule small (5 µm) 2

2 Male P5 curved, not trapezoid. Male rostrum U-shaped in ventral view. Ventrolateral band on cephalosome not net-like ..... *Kensakia parva* Harris & Iwasaki, 2009

—— Male P5 trapezoid. Male rostrum V or Y-shaped in ventral view. Ventrolateral band on cephalosome net-like 3

3 Female maximum length < 0.65 mm. Female cephalosome width/rostrum ratio < 4.2. Labrum with pad of minute setules + four lateral striations. Female carries eight eggs. (Plate 1D .....*Kensakia australis* sp. nov.

—— Female maximum length > 0.75 mm. Female cephalosome width/ rostrum ratio > 4.5. Labrum without pad of fine setules or striations. Female carries 16–18 eggs. (Plate 2F) ..... *Kensakia acuta* (Kim & Kim, 1997)

Kensakia australis sp. nov.

Figs 13, 14; Plate 1D

Type material. Holotype adult male, length 0.55 mm, P81210. allotype adult female, length 0.62 mm, P81211. Paratype specimens P81212 (10 ♀♀, 5 ♂♂) deposited at AM, Sydney. Additional paratypes deposited at NHM, London. All collected from a brown seaweed, Zonaria sp., sublittoral fringe, Point Vernon, Hervey Bay, Queensland (25°15'S 152°47'E), V. A. Harris 1997.

Diagnosis. Labrum with medial pad of minute setules plus four or five lateral striations (ridge-plates absent); female rostrum broad (W/R = 4.1); females carry eight eggs; male antennule with transverse tunnel-like thickening of cuticle on ventral side of segment 4 (Fig. 13E), distal coupling denticle very small (3–5 µm), dactylus long (= length of segment 3+4), hooked distally; ventrolateral band on ventral side of cephalosome with net-like markings; very few dorsal sensilla; no setae lateral to female genital opening; male rostrum V-shaped ventrally; α and β setae on male caudal ramus short (½ width of ramus); ventral setules on male anal segment; dorsal setae on female P5 not pinnate.

Biometric data. *Females* (N = 25): maximum length (L_{max}) mean 0.615 mm, range 0.58–0.65 mm, body length (L_{urs}) mean 0.58, range 0.56–0.61 mm; cephalosome width (W) mean 0.37 mm; rostrum (R) width 0.09 mm; genital double-somite width 0.186 mm, length 0.145 mm; caudal ramus maximum width 0.05 mm, length 0.135 mm,

Ratios: L_{urs}/W 1.57, L_{max}/W 1.66; W/R 4.1; genital double-somite w/l 1.27, arch 55% of length; caudal ramus 22% of L_{urs}, l/w 2.6, Hicks' index for α 88%, for β 76%, apex angle of ramus 42°.

Males (N = 23): maximum length (L_{max}) mean 0.55 mm, range 0.55–0.58 mm, body length (L_{urs}) mean 0.51, range 0.49–0.64 mm; cephalosome width (W) mean 0.34 mm, range 0.31–0.37 mm, length 0.32 mm; rostrum length 0.045 mm; caudal ramus width 0.04, length 0.05 mm; antennule (fully extended) 0.145 mm; spermatophore 0.078 × 0.02 mm.

Ratios: L_{urs}/W 1.5, L_{max}/W 1.6; cephalosome 58% of L_{max}; caudal ramus l/w 1.25; antennule 26% of body length L_{urs}, segments 3+4 41%, dactylus 43%, aesthetasc 70% of antennule length; spermatophore 14% of L_{urs}.

Description. *Adult females* (Fig. 13A; Plate 1D, p. 163): colour pale yellow or colourless, mid-dorsal area of cephalosome, metasome and genital double-somite dark blue-purple, caudal rami and P5s not coloured. Cephalosome semicircular, rostrum broad, not prominent, dorsal pits on cephalosome, metasome, genital double-somite and P5 exopod small (3–5 µm), very few dorsal sensilla. Hyaline border clear, 6–7 µm wide. Ducts of marginal glands open dorsally. On ventral side of cephalosome there is a broad lateral band of net-like markings about 30 µm wide that narrows posteriorly (ventrolateral band, Fig. 13J) and a peripheral band of vacuous cells (seen from ventral side Fig. 13H). Some specimens have reticulate markings on ventral surface of the rostrum. Labrum (Fig. 14J) with pad of minute hair-like setules and a group of four or five setules laterally, but no ridge plates. Genital double-somite (Fig. 14C) narrow (50% of cephalosome width), lateral border with fine setules, small notch marks boundary between anterior and posterior lobes, posterior lobe pointed posteriorly, arch deep, no anterolateral ridges (rugosities) present. Sternal sclerite of metasome segment 4 with fimbriate posterior border, genital opening narrow (35 µm), no seta at lateral corner of opening. Caudal ramus (Figs 13D) trapezoid (sides slightly divergent), maximum width ⅔ down ramus, lateral and medial edges without setules, dorsal surface with net-like pattern. α and β setae close, terminal setae T1 and T4 plain, very small, setae T2 and T3 absent, posterior border with very short, fine setules. Structure and setation of mouthparts and ambulatory limbs typical of family. Antenna basis with triangular setules along anterior edge but no setules on lateral surface (Fig. 14B), exopod with five plumulose setae and one plain spinous seta, fine border setules on segment 1 of endopod, segment 2 with three lateral setae, end segment of geniculate setae plain, long thin comb-like claw (> ⅓ length of endopod segment 2). Mandible, maxillule and maxilla as shown in Figs 14G, I and K respectively, maxilliped (Fig. 14L) basis with fimbriate border but no rows of small lateral setules. P1 (Fig. 13C) with coxal seta, inconspicuous small patch of denticulate pegs at lateral end of fimbriate crescent. Serrulate spinous seta on segment 2 of P3 endopod (Fig. 14E) shorter than endopod (0.8:1), large serrate spinous seta on segment 3 much longer than endopod (1.5:1). P4 endopod with serrulate spinous seta on segment 2 and 3 (Fig. 14D). Exopod of P5 lanceolate, without ventral expansion, dorsal surface pitted, apical end of ventral falciform ridge with concave notch (Fig. 14A), border setules short, two prominent dorsal setae and two apical setae. P5s extend beyond genital double-somite and caudal rami but do not touch posteriorly. Females carry eight eggs.

Adult males (Fig. 13B). Colour similar to female except that the blue-purple dorsal area does not extend beyond metasome segment 2. Cephalosome truncated with sloping, rounded shoulders, lateral angle of antennule socket prominent. Rostrum narrow, keeled and Y-shaped in ventral view, width ⅔ of length (Fig. 14M). Dorsal pits, hyaline border, vacuolated cells, reticulate ventral band and labrum as for female. Caudal rami (Fig. 14H) rectangular, slightly longer than wide (1.2:1), dorsal surface with net-like markings, α and β setae short (< ½ width of ramus). Setae T1, T2 and T4 very short and small (T2 and T4 lost on many specimens), T3 absent. Posterior border with very short setules. Small group of striations (5 or 6) on ventral side of anal segment at the posterolateral corner (Fig. 14H). Antennule (Fig. 13F) with pinnate seta on segment 1, distal coupling denticle on segment 4 small (3–5 µm) bicuspid, close to brush-pad, aesthetasc almost as long as segment 3+4 + dactylus with two characteristic constrictions, dactylus equals length of segment 3+4, hooked at tip (Fig. 13F, G). A tunnel like indentation of the ventral cuticle is found on the ventral side of segment 4 just proximal to the sensory lobe carrying aesthetasc (Fig. 13E, "tunnel"). Limbs as for female except that P2 has only two terminal setae on the endopod. All setae on P4 endopod plumose. P5 exopod trapezoid, lateral seta with row of 12–15 ventral setules and of different shape to terminal setae (Fig. 14F). Spermatophore very small.

Etymology. The first species belonging to *Kensakia* recorded from Australia.

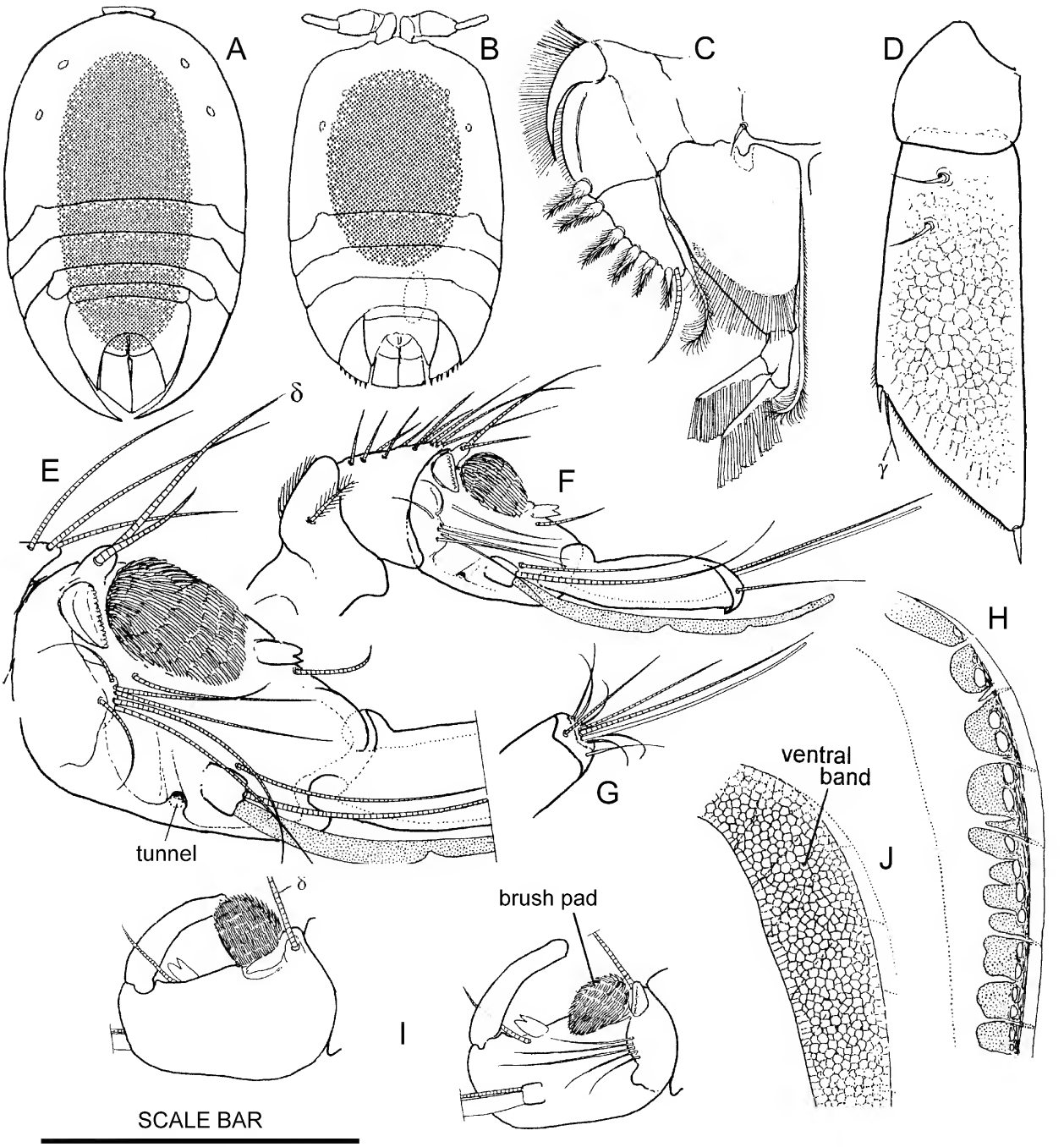

Figure 13. *Kensakia australis* sp. nov. Female: *(A)* adult; *(C)* P1; *(D)* caudal ramus. Male: *(B)* adult; *(E)* antennule (ventral, showing "tunnel"); *(F)* antennule; *(G)* antennule segment 6; *(H)* cephalosome border showing vacuolated cells; *(I)* antennule brush pad (dorsal, ventral); *(J)* underside of cephalosome showing ventrolateral band. Scale bar: A, B = 0.48 mm. C = 0.12 mm. D, F, I = 0.11 mm. E, G = 0.05 mm. H, J = 0.10 mm.

Remarks. *Kensakia australis* closely resembles Japanese specimens of *K. acuta* but is significantly smaller, differs slightly in colour pattern, shape of female rostrum and in the number of eggs carried in each brood.

Distribution. *Kensakia australis* is common at low water spring tides at Hervey Bay, Queensland on *Zonaria* sp. Type series (PV3, 7/97, 76 ♀♀ + 65 ♂♂) and *Eucheuma* sp., (PV6, 60 ♀♀ + 23 ♂♂ + juveniles), V. A. Harris 1997. It has also been recorded from *Dilophus* sp., and *Lobophora* sp., in rock pools at Arrawarra, NSW (30°03'S 153°02'E), V. A. Harris, 1982.

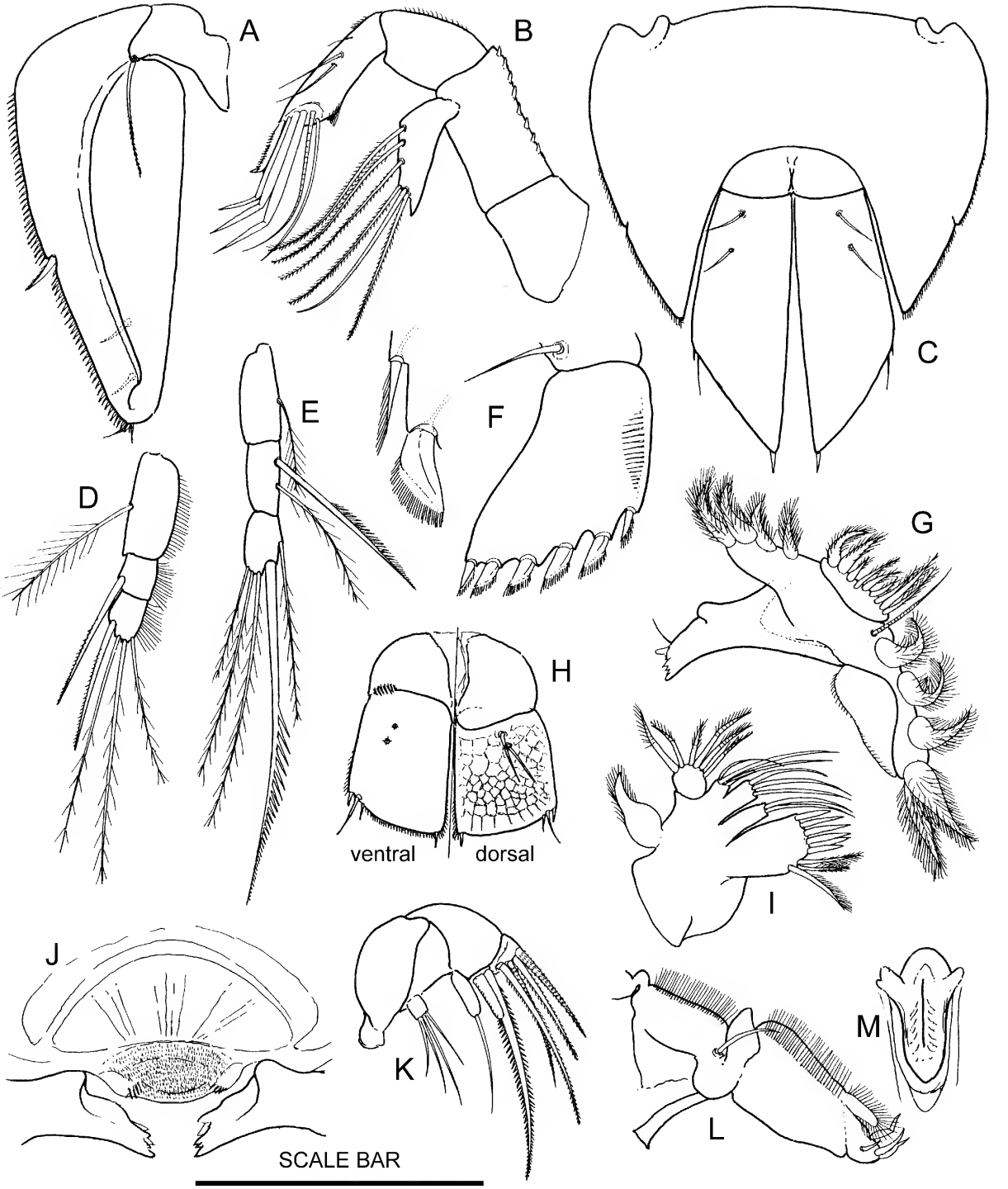

Figure 14. *Kensakia australis* sp. nov. Female: *(A)* P5 (ventral); *(B)* antenna; *(C)* genital double-somite and caudal rami; *(D)* P4 endopod; *(E)* P3 endopod; *(G)* mandible; *(I)* maxillule; *(J)* labrum; *(K)* maxilla; *(L)* maxilliped. Male: *(F)* P5 (ventral, detail of lateral and terminal setae); *(H)* caudal rami and anal segment; *(M)* rostrum (ventral). Scale bar: A, B = 0.18 mm. C = 0.14 mm. D, I, J, K, L = 0.08 mm. E, F, H = 0.1 mm. G = 0.12 mm.

Genus *Kushia* Harris & Iwasaki, 1996

Kushia Harris & Iwasaki, 1996: 204.—Bodin, 1997: 68; Walker-Smith, 2001:655; Wells, 2007: 80.
Porcellidium.—Gamô, 1969: 345; Kim & Kim, 1997: 161.

Type species. *Kushia zosteraphila* Harris & Iwasaki, 1996.

Diagnosis. Female P5 exopod with ventral expansion that lies under (ventral to) edge of genital double-somite (Fig. 16E); male antennule with conspicuous anterior comb near δ seta on segment 3, and three coupling denticles on segment 4 (middle denticle expanded distally, Y-shaped Fig. 18E, F), no brush-pad; hyaline border with sensilla at lateral edge of cephalosome, marginal glands conspicuous with ducts opening dorsal to border; no massive dorsal cuticular honeycomb; no ridge-plates on labrum; no lateral striations on female genital double-somite; female caudal rami pentagonal, typically widen posteriorly, terminal setae T1 to T4 all present, not pinnately clavate or evenly spaced; maxillule endopod with six setae; coxae of maxillipeds touch in mid-line; male P5 trapezoidal with six terminal setae; spermatophore elongate, ephemeral on female.

Species composition. *Kushia zosteraphila* Harris & Iwasaki, 1996; *K. gamoi* Harris & Iwasaki, 1996; *K. igaguria* Harris & Iwasaki, 1996; *Kushia spathoides* sp. nov.

The genus is known from Japan, Korea and northern NSW, Australia.

Etymology. The name *Kushia* refers to the characteristic anterior comb on male antennule, (Japanese *Kushi* a type of Japanese hair comb).

Remarks. The genus is clearly defined by structure of male antennule and female P5 limb. The marginal glands possessed by all members of the Porcellidiidae are particularly conspicuous in the above four species. They also occur in other parts of the body such as the genital double-somite, caudal rami and P5 limbs.

Key to the species of *Kushia*

1	Hyaline border of cephalosome clear (not striated). Male cephalosome sharply truncated with angular shoulders 2
——	Hyaline border with striations. Male cephalosome not sharply truncated, shoulders smoothly rounded. (Plate 1I, p. 163) ..... *K. spathoides* sp. nov.
2	First dorsal seta on female P5 very small or absent. Truncated anterior of male cephalosome straight. No setules at base of terminal setae on male P5 3
——	First dorsal seta on female P5 long, (same length as seta two & three). Truncated anterior of male cephalosome concave. Rows of 7–10 setules at base of each terminal seta on male P5. (Plate 2D, p. 165) ..... *K. zosteraphila* Harris & Iwasaki, 1996
3	Female caudal ramus with parallel sides*. Proximal denticle on segment 4 of male antennule flat with serrated edge. Colouration uniform pale orange-brown ..... *K. gamoi* Harris & Iwasaki, 1996
——	Female caudal rami widen posteriorly*. Proximal denticle on segment 4 of male antennule rounded and covered with spine-like setules. Colouration pale yellow-brown with metasome and genital double-somite darker orange-brown. (Plate 2C, p. 165) ..... *K. igaguria* Harris & Iwasaki, 1996

* Caudal ramus laid flat.

Kushia spathoides sp. nov.

Figs 15–18, Plate 1I

Type material. HOLOTYPE adult male, length 0.68 mm, P81204; ALLOTYPE adult female, length 0.75 mm, P81205; PARATYPE specimens, 5 ♀♀, 5 ♂♂, P81206, deposited at AM, Sydney. Additional paratypes deposited at NHM, London. All collected at Arrawarra Headland, Woolgoolga, northern NSW, Australia (30°06'S 153°02'E), washed from *Caulerpa vesiculifera* in coral rockpool, V. A. Harris, 1982.

Diagnosis. Striations in hyaline border close to edge of cephalosome (Fig. 15E); male cephalosome rounded anteriorly (very slight truncation), shoulders smoothly rounded; anterior comb on male antennule short (length about twice width), small finger-like ventral process lies between anterior comb and π setae on segment 3 of male antennule (Fig. 18F), proximal coupling denticle on segment 4 flat with serrate edge, middle denticle Y-shaped with plain edge, dactylus not bent or hooked distally; female caudal ramus widens posteriorly, T1 recessed at lateral corner to give ramus pentagonal appearance; dorsal seta 1 on female P5 exopod very small, seta 2 large (Fig. 16D).

Biometric data. *Females* (N = 10): maximum length (L_{max}) mean 0.75 mm, range 0.72–0.76 mm, body length (L_{urs}) mean 0.71 mm, range 0.69–0.72 mm; cephalosome width (W) mean 0.48 mm, range 0.45–0.51 mm; rostrum (R) 0.095 mm; genital double-somite width 0.27 mm, length 0.20 mm; caudal ramus width (mean) 0.055 mm, length 0.11 mm.

Ratios: L_{urs}/W 1.46, L_{max}/W 1.54; cephalosome W/R 5.1; genital double-somite w/l 0.73, arch 40% of length; caudal ramus 15% of L_{urs}, l/w 2.0, Hicks' index for α 73%, for β 55%.

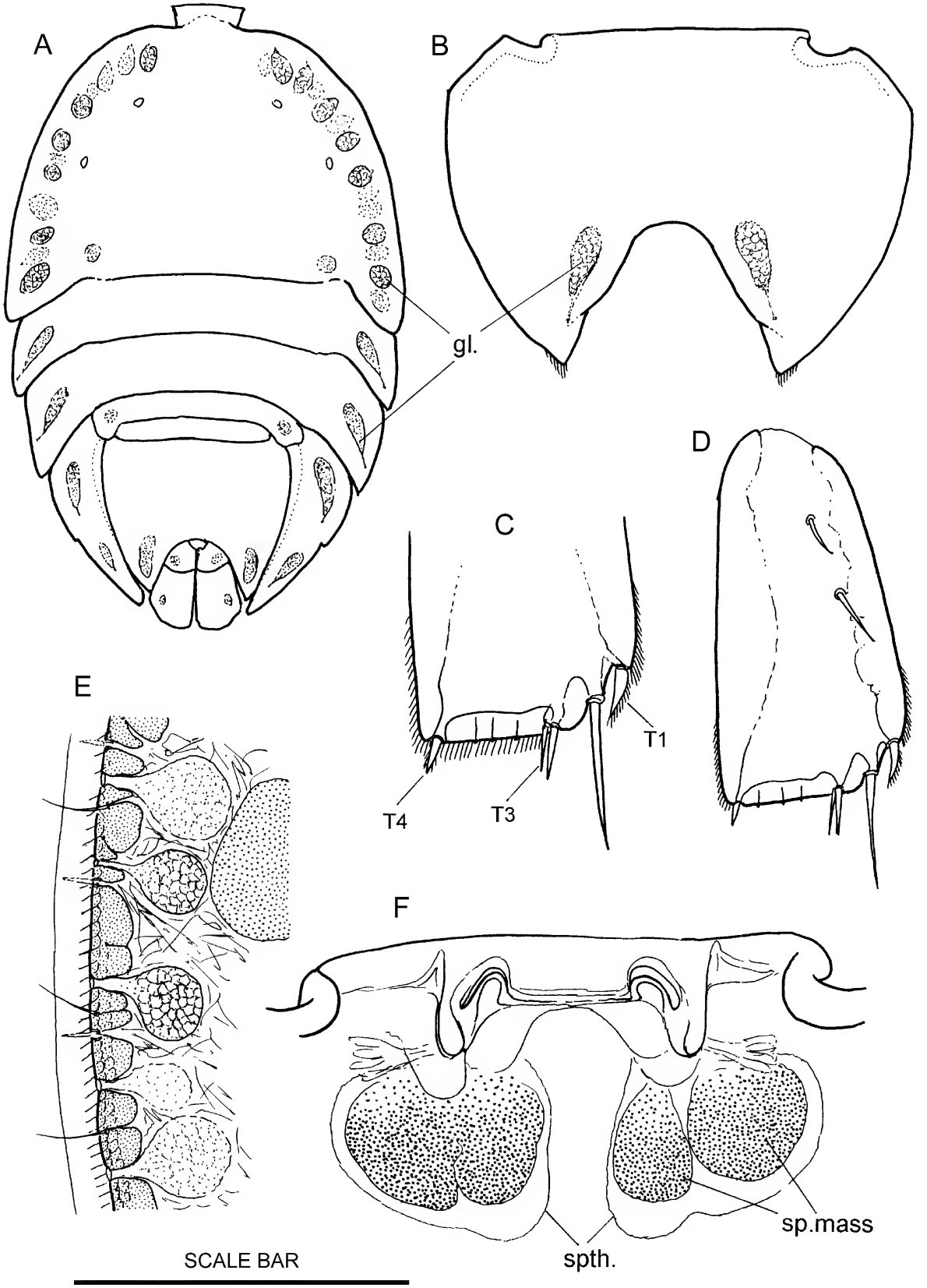

Figure 15. *Kushia spathoides* sp. nov. Female: *(A)* adult showing distribution of marginal glands (*gl.* marginal glands); *(B)* genital double-somite; *(C, D)* caudal ramus; *(E)* edge of cephalosome showing striations; *(F)* genital opening showing spermathecae *(spth.)* and sperm mass *(sp. mass)*. Scale bar: A = 0.45 mm. B, D, E, F = 0.1 mm. C = 0.06 mm.

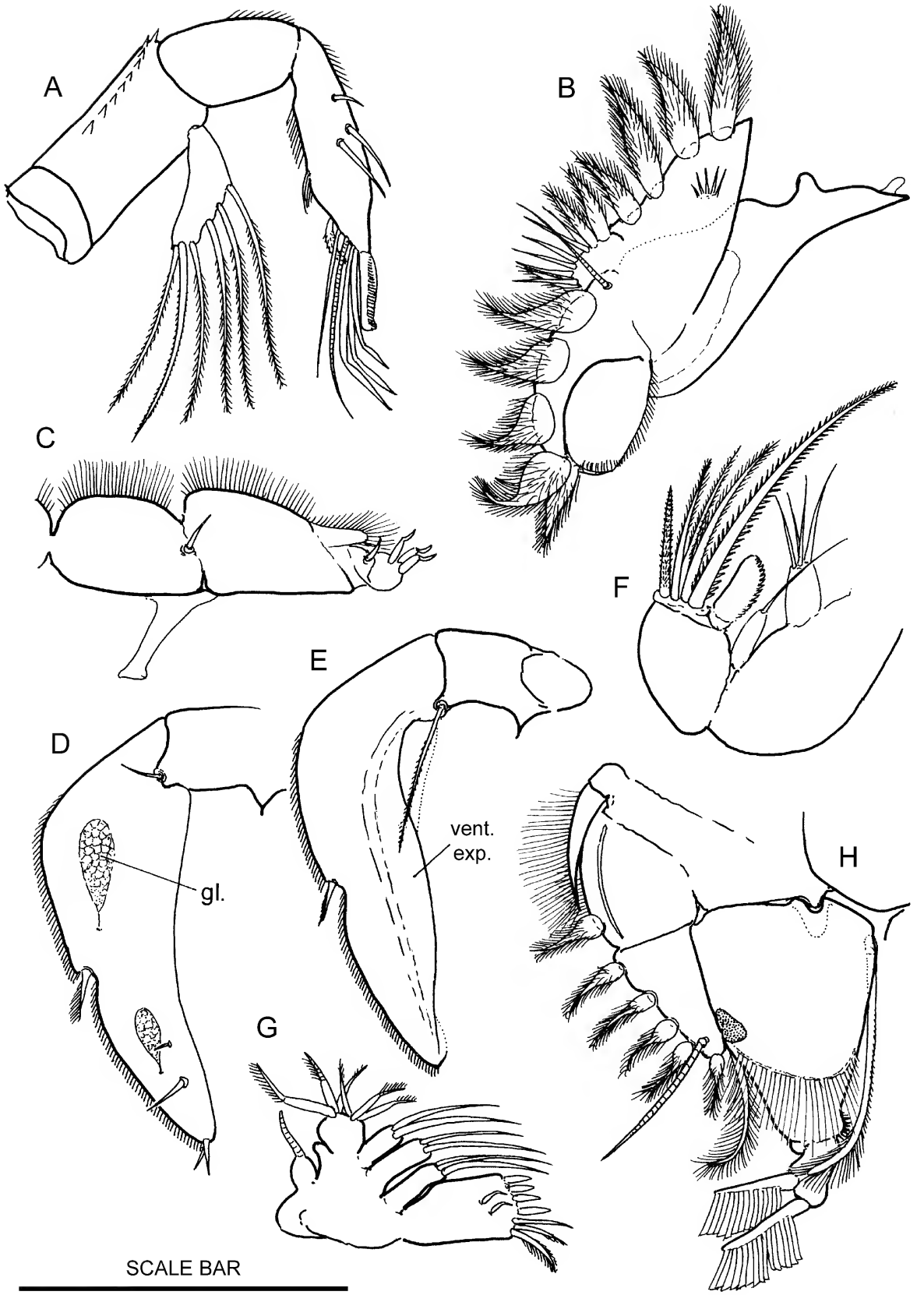

Figure 16. *Kushia spathoides* sp. nov. Female: *(A)* antenna; *(B)* mandible; *(C)* maxilliped; *(D)* P5 (dorsal, *gl.* marginal glands); *(E)* P5 (ventral, showing ventral expansion, *vent.exp*); *(F)* maxilla; *(G)* maxillule; *(H)* P1. Scale bar: A = 0.08 mm. B = 0.2 mm C = 0.09 mm. D. E = 0.18 mm. F, H = 0.12 mm. G = 0.1 mm.

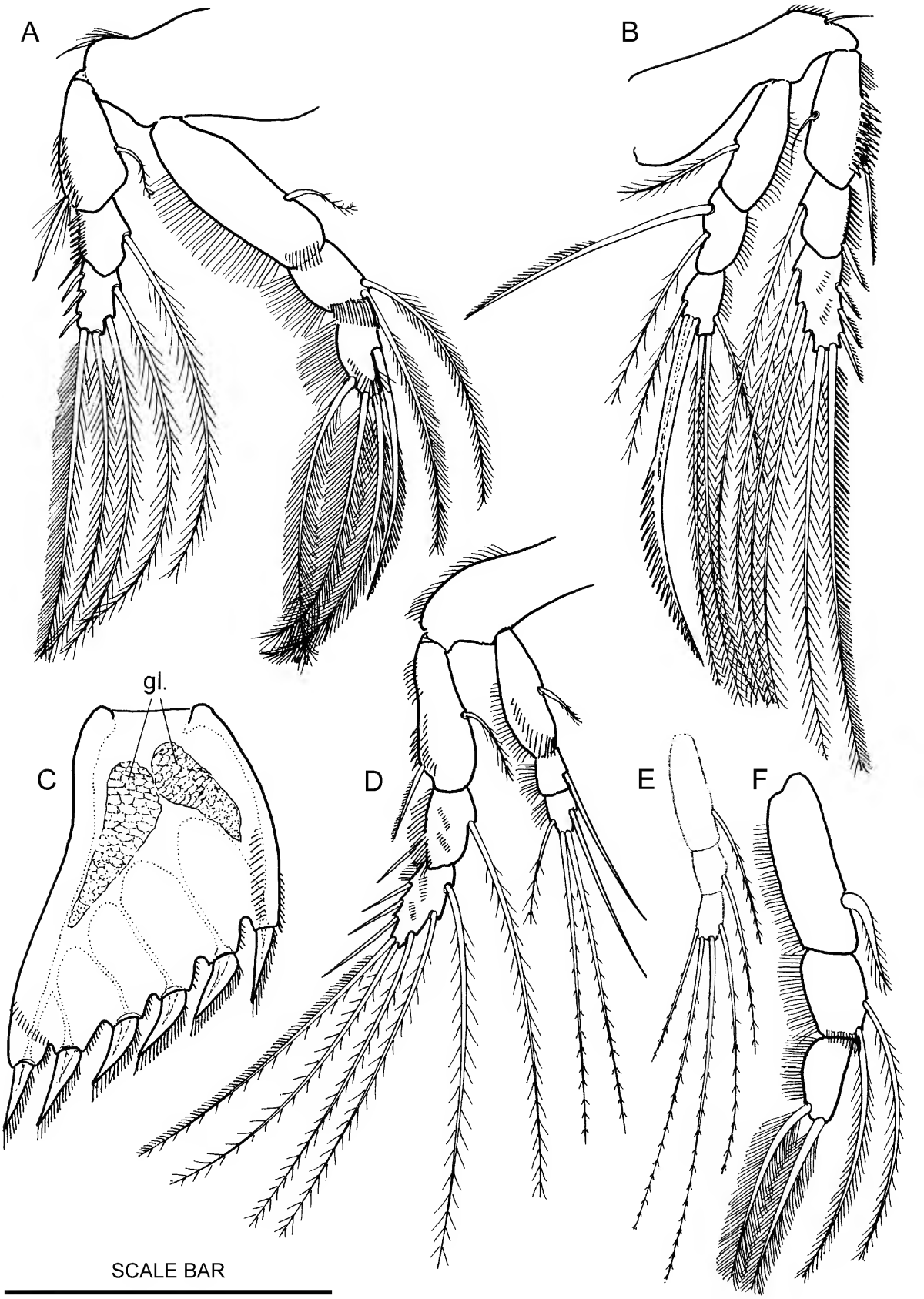

Figure 17. *Kushia spathoides* sp. nov. Female: *(A)* P2; *(B)* P3; *(D)* P4. Male: *(C)* P5 (ventral, *gl.* marginal glands); *(E)* P4 endopod; *(F)* P2 endopod. Scale bar: A, B, D, E, F = 0.14 mm. C = 0.1 mm.

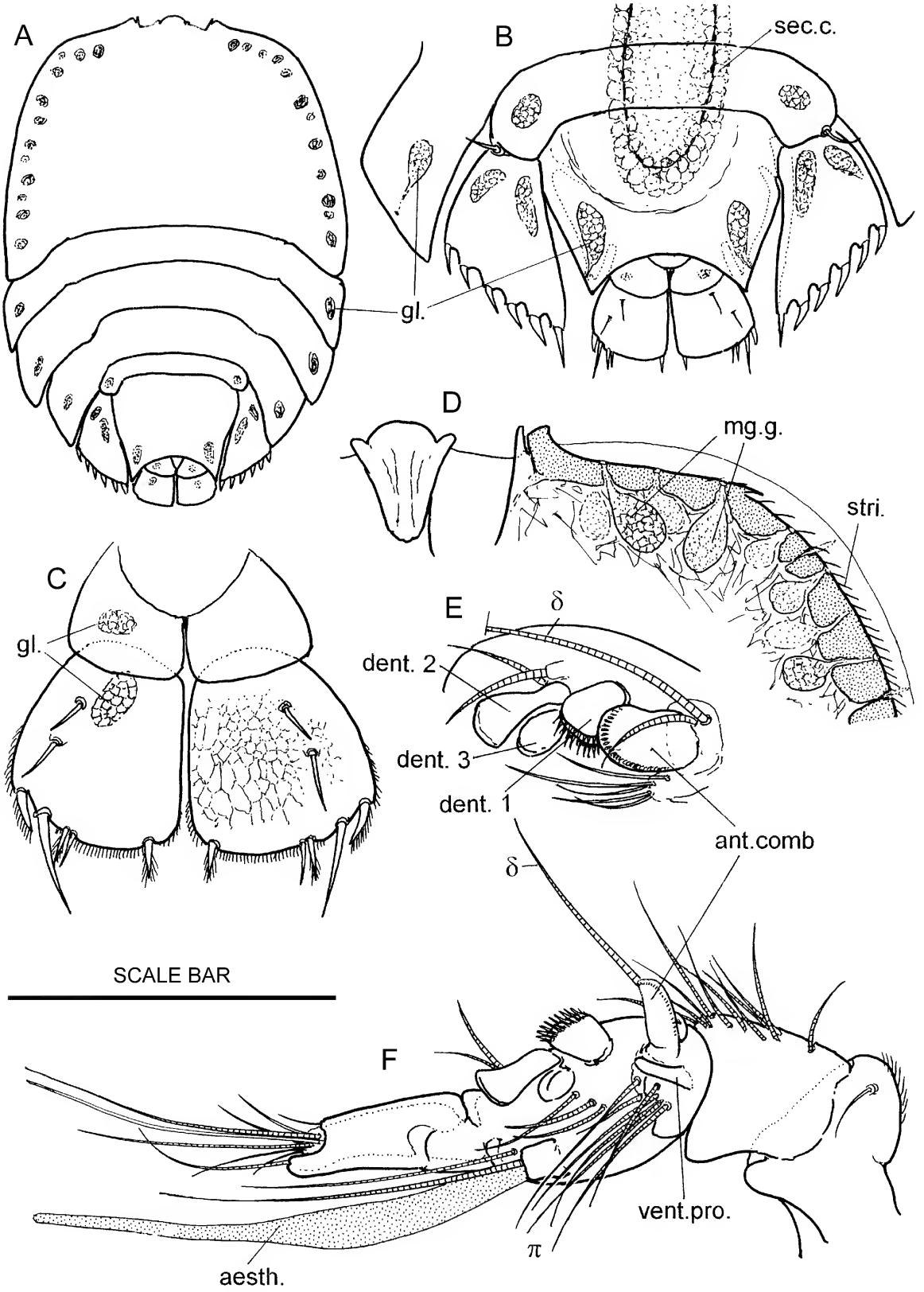

Figure 18. *Kushia spathoides* sp. nov. Male: *(A)* adult (*gl.* marginal glands); *(B)* abdominal region and caudal rami showing secretory cells *(sec.c.)* producing spermatophore case; *(C)* caudal rami; *(D)* rostrum and "shoulder" (ventral; *mg.g.* marginal gland; *stri.* striations); *(E)* coupling denticles *(dent.)* of antennule; *(F)* antennule, showing anterior comb *(ant.comb)* and ventral process *(vent.pro.)*. Scale bar: A = 0.45 mm. B = 0.23 mm. C, F = 0.1 mm. D = 0.14 mm. E = 0.08 mm.

Males (N = 7): maximum length (L_{max}) mean 0.68 mm, range 0.66–0.70 mm, body length (L_{urs}) mean 0.63 mm, range 0.62–0.67 mm; cephalosome width (W) mean 0.46 mm, range 0.43–0.47 mm, length 0.35 mm; caudal ramus width 0.05 mm, length 0.05 mm; antennule (fully extended) 0.19 mm, length of anterior comb on antennule 0.02 mm; spermatophore 0.23 × 0.07 mm.

Ratios: L_{urs}/W 1.38, L_{max}/W 1.47, cephalosome 52% of L_{max}; caudal ramus l/w 1.0; antennule 28% of body length; segment 3+4 40%, dactylus 33% of antennule length; spermatophore 34% of L_{max}.

Description. *Adult females* (Fig. 15A; Plate 1I, p. 163): colour pink. Body outline elliptical, rostrum prominent, narrow. Dorsal pits conspicuous (4–6 μm), hyaline border (8 μm wide) appears striated due to edge of overlapping pits that project about 4 μm over hyaline border (Fig. 15E, 18D). Twelve or more conspicuous marginal glands on each side of the cephalosome with ducts that open just above hyaline border (Figs 15A,E, 18A,D). Similar glands are found in the epipleura of metasome segments, genital double-somite, caudal rami and P5 limbs. Dorsal surface of genital double-somite with pits, lateral border smoothly curved without notch or scar to indicate boundary between anterior and posterior lobes, border setules absent except for a few short setules at pointed posterior extremity, arch less than half length of genital double-somite (Fig. 15B). Genital opening as shown in Fig. 15F. Labrum without ridge plates. Caudal rami (Fig. 15D) widen posteriorly (maximum width about ⅘ down ramus), dorsal surface with faint reticulation. Beta seta almost half way down ramus, γ seta slightly recessed on posterior border, T1 recessed at lateral corner, T2 and T3 setae extremely close, T4 short at medial corner, posterior border thickened with three dorsal ridges (Fig. 15C), fine setules along posterior border. Structure and setation of mouthparts and ambulatory limbs typical of family. Antenna (Fig. 16A) basis with diagonal row of triangular setules, marginal setules on segments 1 and 2 of endopod, exopod with five finely plumulose setae and one spinous seta, three lateral setae on segment 2 of endopod, geniculate setae with plain terminal section, small sensory structure present, claw comb-like. Mandible (Fig. 16B) with small group of setules on anterior lobe of palp. Maxillule (Fig. 16G) with single seta on exopod. Maxilla and maxilliped as in (Fig. 16F, C). P1 endopod segment 1 narrow (l/w = 1.28), (Fig. 16H) with small triangle of denticulate setules at lateral corner of fimbriate crescent. Serrulate spinous seta on segment 3 of P2 endopod ¾ length of endopod (Fig. 17A). Serrulate spinous seta on segment 2 of P3 endopod (Fig. 17B) equal in length to endopod (1:1), large serrate spinous seta on segment 3 longer than endopod (1.35:1). Endopod of P4 with a plain spinous seta on segment 2 and similar first internal seta on segment 3 (Fig. 17D). Baseoendopod of P5 with triangular prominence on posterior border (Fig. 16D), exopod lanceolate, dorsal surface with pits, ventral expansion below falciform ridge (Fig. 16E) lies under edge of genital double-somite, first dorsal seta very small or absent, second seta long, apex with two setae. Females carry 12 eggs.

Adult males (Fig. 18A). Colour pink. Anterior of cephalosome rounded, only slightly truncated, shoulders smoothly rounded, lateral angle of antennule socket prominent. Hyaline border, marginal glands and border striations as for female (Fig. 18D). Caudal rami (Fig. 18C) widen posteriorly (maximum width almost twice proximal width), lateral and posterior border convex, length equal to maximum width, dorsal surface with faint reticulate pattern. Setation similar to female, but posterior border without three dorsal ridges. Antennule (Fig. 18F), anterior comb on segment 3 broad (spatulate), small finger-like ventral process present between anterior comb and π setae. First coupling denticle flat with double row of serrations along edge, second denticle longer, widens distally, without serrated edge, third denticle circular without serrated edge (Fig. 18E). Dactylus straight, ¾ length of segment 3+4, no terminal hook. Aesthetasc very long (about ¾ length of antennule). Limbs as described for female except for the following differences. P2 with two plumose terminal setae on segment 3 of endopod (Fig. 17F). Terminal spinous seta on P3 endopod equal in length to endopod. P4 endopod setae not spinous (Fig. 17E). P5 trapezoid (Fig. 17C), dorsal surface with pits, about 15 fine ventral setules at base of first (lateral) seta, diagonal row of five or six setules at base of each terminal seta. Spermatophore large (⅓ body length). Cells secreting spermatophore capsule shown in Fig. 18B.

Etymology. The trivial name, *spathoides*, refers to the broad spatulate anterior comb on segment 3 of the male antennule (G. *spathe* = ladle or spatula + *oides* = shape). It contrasts with the long narrow comb on Japanese species.

Remarks. The genus *Kushia* is known from Japan, but *K. spathoides* is the first record for Australia.

Distribution. This species was collected from *Caulerpa vesiculifera* growing in a coral rock pool at Arrawarra Head, NSW, but was not found at Nambucca Heads (60 km south) or Ballina (140 km north). All females in type series, (Aw14,11/82, 42 ♀♀, 41 ♂♂, 26 juveniles) carry eggs, nine of the males were coupled to juvenile females, V. A. Harris 1982.

Genus *Acutiramus* Harris & Robertson, 1994

Acutiramus Harris & Robertson, 1994: 288.—Bodin, 1997: 67.
Kioloaria Harris, 1994.—Bodin, 1997: 67.
Porcellidium.—Thompson & Scott, 1903: 275; Geddes, 1968: 11; Humes & Ho, 1969:115; Hicks & Webber, 1983: 439; Ho, 1986: 21; Kim & Kim, 1996: 376; Walker-Smith, 2001: 655; Wells, 2007: 80.

Type species. *Acutiramus rufolineatus* Harris & Robertson, 1994: 289.

Diagnosis. No anterior comb or denticle near δ seta on male antennule segment 3, typically two coupling denticles on segment 4; female caudal ramus typically rhomboid but may taper distally; terminal setae T1 to T4 always present, T4 at posterior apex; six setae on maxillule endopod; coxae of maxillipeds touch in midline; no ventral expansion to female P5, P5 limbs reach beyond genital double-somite and caudal rami to touch one another posteriorly; spermatophore elongate, ephemeral on female.

Species composition. Species possessing these features fall into two distinct groups—those living as inquilines or commensals with hermit crabs and those free living on algae.

The commensal group do not have an internal seta on segment 1 of P3 endopod.

Acutiramus brevicaudatus (Thompson & Scott, 1903); *A. tapui* (Hicks & Webber, 1983) comb. nov.; *A. paguri* (Ho, 1986) comb. nov.; *A. similis* (Kim & Kim, 1996) comb. nov.; *A. cumulus* sp. nov.; *A. iwasakii* sp. nov.

The algal group have an internal seta on segment 1 of P3 endopod.

Acutiramus geddesi (Geddes, 1968) comb. nov. (synonym *Porcellidium ovatum* Geddes, 1968); *A. rufolineatus* Harris & Robertson, 1994; *A. quinquelineatus* Harris & Robertson, 1994; *A. sesquimaculatus* (Harris, 1994) comb. nov.; *A. bipunctatus* sp. nov.; *A. edenensis* sp. nov.

Genus known from Indian Ocean, Madagascar, Ceylon, Pacific Ocean, Japan, Korea, Australia, New Zealand and Bahamas.

Remarks. Although no clear apomorphic character defines *Acutiramus*, the genus is clearly separated from *Porcellidium* by a unique combination of characters and is excluded from all other genera by their own apomorphies. Relative to cephalosome width (W), the genital double-somite width (w) of *Acutiramus* is narrower than that of *Porcellidium* (mean w/W for *Acutiramus* = 48%, range 40–53%, N = 10 species: for *Porcellidium* w/W = 62%, range 55–63%, N = 18 species) and the posterior lobe is narrow and pointed compared with the broad, rounded posterior lobe of *Porcellidium* species. A characteristic feature of all female members of the genus is the long P5 limb that extends beyond the posterior limit of the caudal furca. On living or freshly preserved animals the posterior apices appear to touch, but when mounted on a slide the pressure of the cover glass usually separates them as shown in Figure 27A. *Synurus* and *Kensakia* also have P5 limbs that are longer than the caudal furca and may touch posteriorly, but their defining apomorphic characters eliminate *Acutiramus* species.

Porcellidium ovatum Haller, 1879 is a synonym of *Porcelloides tenuicaudus* (see Harris, 2014), but the animals identified by Geddes (1968) as *Porcellidium ovatum* do not show the characteristic features of *Porcelloides tenuicaudus,* i.e., female body shape is oval, not ovoid; caudal ramus rhomboid, not trapezoid; terminal seta T3 is present; genital double-somite is deeply cleft and its arch encloses half the caudal furca; dorsal setae on P5 are plain, not pinnate. Moreover, Geddes' female is less than half the size (0.62 mm compared with 1.4 mm). The shape and setation of the female caudal ramus and length of P5 eliminate Geddes' animals from *Porcellidium* and the presence of T3 eliminates them from *Ravania* and *Kensakia*. They are included here as *Acutiramus geddesi* (Geddes, 1968) comb. nov.

Walker-Smith (2001) argues that the genus *Kioloaria* possesses the same character set as *Acutiramus* except for the number of setae on male P2 limb. This character cannot be considered apomorphic because it occurs sporadically in other genera and so there is no justification for maintaining *Kioloaria*. This argument is accepted, although *K. sesquimaculata* does have an unusual male antennule. It is moved to *Acutiramus* as *A. sesquimaculatus* (Harris, 1994). *Kioloaria* now becomes a junior synonym of *Acutiramus.*

Key to the species of *Acutiramus*

1	No internal seta on segment 1 of P3 endopod. Animals live in association with hermit crabs 2
——	Internal seta present on segment 1 of P3 endopod. Animals live on seaweed 6
2	Female caudal ramus rhomboid, T2 and T3 close together, wide gap between T3 and T4. Male shoulders rounded 3
——	Female caudal ramus not rhomboid, tapers posteriorly, posterior edge rounded, no network of ridges (if present not prominent, restricted to posterior). T2, T3 and T4 evenly spaced. Male shoulders rounded ..... *Acutiramus tapui* (Hicks & Webber, 1983) comb. nov.
——	Female caudal ramus rhomboid with conspicuous dorsal network of ridges, T2, T3 and T4 bunched together at apex. Male shoulders prominent ..... *Acutiramus cumulus* sp. nov.
3	¼ or more of caudal ramus enclosed in arch of genital double-somite 4
——	Caudal ramus completely excluded from arch of genital double-somite ..... *Acutiramus brevicaudatus* (Thompson & Scott, 1903)
4	Number of setae on internal edge of P3 endopod = 0:2:4, P4 endopod = 0:1:3 ..... *Acutiramus paguri* (Ho, 1986) comb. nov.
——	Number of setae on internal edge of P3 endopod = 0:2:5, P4 endopod = 1:1:4 5
5	Female rostrum appears concave with straight hyaline border. Male rostrum with conspicuous anterior point. γ seta on male caudal ramus equals width of ramus ..... *Acutiramus iwasakii* sp. nov.
——	Anterior border of female rostrum not concave. Male rostrum not pointed anteriorly. γ seta on male caudal ramus twice width of ramus ..... *Acutiramus similis* (Kim & Kim, 1996)

6 α and β setae on female caudal ramus not close (equal to or greater than ⅓ length of ramus apart). Male P5 trapezoid (sides not parallel) 7

—— α and β setae on female caudal ramus not close (equal to or greater than ⅓ length of ramus apart). Male P5 rhomboid (sides parallel). Male P2 endopod with two terminal setae ..... *Acutiramus geddesi* (Geddes, 1968) comb. nov.

—— α and β setae on female caudal ramus close together (⅛ length of ramus apart). Male P5 trapezoid. Male P2 endopod with three terminal setae. (Plate 2A) ... *Acutiramus sesquimaculatus* (Harris, 1994) comb. nov.

7 Anterior bulge on female cephalosome partly obscures rostrum. Male antennule with ventral blade 8

—— No anterior bulge on cephalosome, rostrum prominent. No ventral blade on male antennule 9

8 Female P5 truncated posteriorly. Female genital double-somite without lateral notch. Ventral blade on male antennule about ½ length of compound segment 3 + 4. (Plate 2B, p. 165) .....*Acutiramus rufolineatus* Harris & Robertson, 1994

—— Female P5 not truncated (P5 laid flat), apex with small notch. Female genital double-somite with distinct lateral notch. Ventral blade on male antennule small (less than ¼ length of segment 3 + 4. (Plate 2E, p. 165) ..... *Acutiramus quinquelineatus* Harris & Robertson, 1994

9 Rostrum with clear spherical "lens". Seta T1 on female caudal ramus very small, T3 very slender, space between T3 and T4 setae ⅔ length of oblique posterior edge of ramus. Coupling denticle on male antennule C-shaped, anterior lobe carrying δ seta short ..... *Acutiramus bipunctatus* sp. nov.

—— No spherical "lens" in rostrum. Seta T1 on female caudal ramus as large as T4, T3 same as T2, space between T3 and T4 setae ½ length of oblique posterior edge of ramus. Coupling denticle on male antennule not C-shaped, anterior lobe carrying δ seta long, finger-like ..... *Acutiramus edenensis* sp. nov.

Acutiramus bipunctatus sp. nov.

Figs 19–22, Plate 1C

Type material. HOLOTYPE adult male, length 0.56 mm, P81192; ALLOTYPE adult female length 0.64 mm, P81193; PARATYPE specimens 15 ♀♀, 10 ♂♂, P81194, deposited at AM, Sydney. Additional paratypes deposited at NHM, London. All collected from *Zonaria* sp., sublittoral, Point Vernon, Hervey Bay, Queensland (25°15'S 152°47'E), V. A. Harris, 1997.

Diagnosis. Conspicuous transparent oval lens-like body in rostrum of male and female; P3 endopod with internal seta on segment 1; space between T3 and T4 setae on female caudal ramus wide (⅔ length of bevelled edge); no plumose setae on segment 2 of male antennule, no ventral blade on segment 3, segment 4 with characteristic C-shaped coupling denticle, dactylus cylindrical (almost as long as segment 3+4); female rostrum prominent, not obscured by median anterior bulge of cephalosome; "shoulders" of male cephalosome rounded, no epaulet present; female caudal ramus long (18% body length), narrow (l/w 3.7), sides straight without setules along medial edge, α and β setae not close, terminal seta T1 to T4 plain, T1 very small, recessed; internal seta present on segment 1 of P4 endopod; female P5 exopod truncated, almost rectangular.

Biometric data. *Females* (N =12): maximum length (L_{max}) mean 0.62 mm, range 0.57–0.68 mm, body length (L_{urs}) mean 0.59 mm, range 0.55–0.63 mm; cephalosome width (W) mean 0.43 mm, range 0.41–0.44 mm; rostrum width (R) 0.10 mm; genital double somite width 0.21 mm, length 0.16 mm; caudal ramus width 0.03 mm, length 0.11 mm.

Ratios: L_{urs}/W 1.39; W/R 4.43; genital double-somite w/l 1.3, arch 50% of somite length; caudal ramus 18% of L_{urs}, ramus l/w 3.7, Hicks' index for β 51%.

Males (N = 11): maximum length (L_{max})mean 0.56 mm, range 0.52–0.58 mm, body length (L_{urs}) mean 0.53 mm, range 0.49–0.55 mm; cephalosome width (W) mean 0.44 mm; caudal ramus width 0.035 mm, length 0.045 mm; antennule fully extended (N = 7) 0.13 mm; spermatophore 0.18 × 0.07 mm.

Ratios: L_{urs}/W 1.2; caudal ramus l/w 1.2; antennule 23% of body length L_{urs}, antennule segment 2 34%, segments 3+4 35% and dactylus 24% of antennule length; spermatophore 30% of body length L_{urs}.

Description. *Adult females* (Fig. 19A; Plate 1C, p. 163): pale yellow or colourless with small pale red dorsal patch immediately behind dark red eyespot, dorsal region of metasome segments pale red. Outline of cephalosome a truncated semi-ellipse with slight dorsal bulge above rostrum, rostrum not obscured. Conspicuous clear oval lens-like body

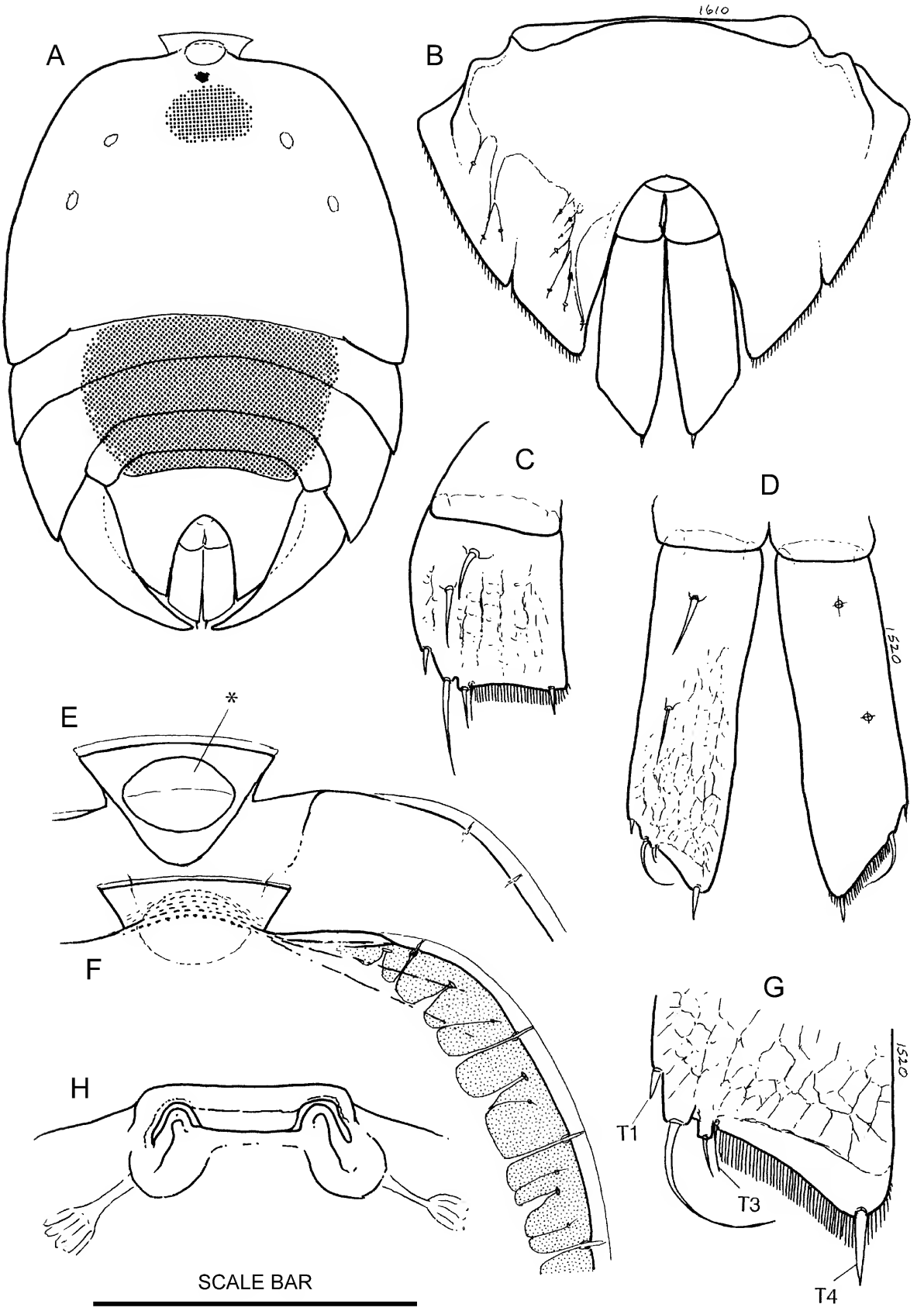

Figure 19. *Acutiramus bipunctatus* sp. nov. Female: *(A)* adult; *(B)* genital double-somite; *(D)* caudal rami; *(E)* rostrum (ventral showing "lens" *); *(F)* rostrum dorsal; *(G)* detail of terminal setae on caudal ramus; *(H)* genital opening. Male: *(C)* caudal ramus. Scale bar: A = 0.34 mm. B, E, F = 0.15 mm. C, H = 0.08 mm. D = 0.1 mm. G = 0.04 mm.

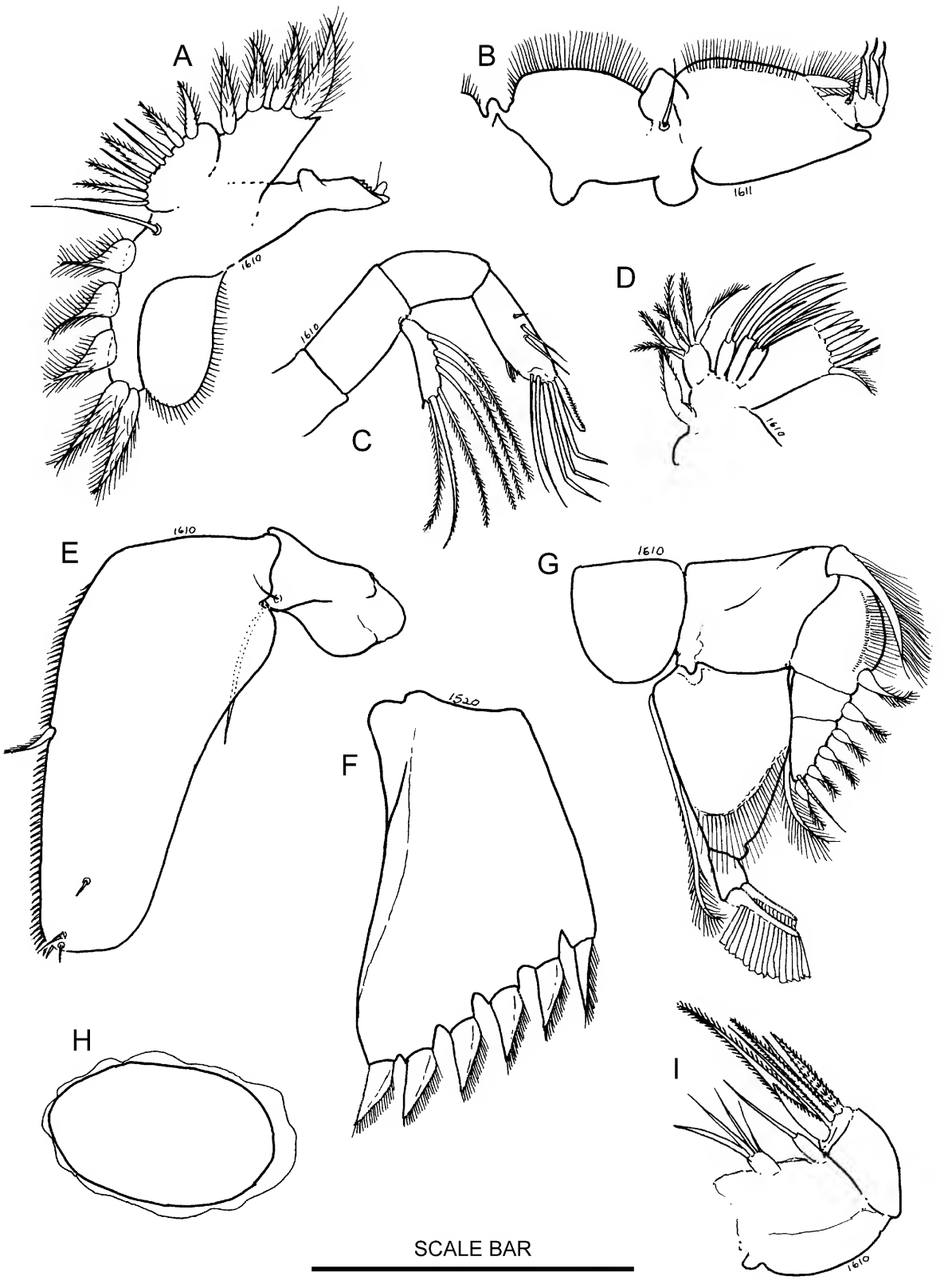

Figure 20. *Acutiramus bipunctatus* sp. nov. Female: *(A)* mandible; *(B)* maxilliped; *(C)* antenna; *(D)* maxillule; *(E)* P5 (dorsal); *(G)* P1; *(H)* isolated egg; *(I)* maxilla. Male: *(F)* P5 (dorsal). Scale bar: A, E = 0.15 mm B, D, F = 0.08 mm C, G = 0.13 mm I = 0.1 mm.

present in rostrum immediately in front of eyespot (Fig. 19E). Dorsal surface with small circular pits 2–3 µm in diameter, low ridges tangential to anterior border. Hyaline border 8 µm wide. Genital double-somite (Fig. 19B) posterior lobes narrow, pointed posteriorly, prominent anterolateral ridge, dorsal surface pitted, edge with fine border setules, notch and short cleft separates anterior and posterior lobes, posterior arch almost half length of genital double-somite, ⅔ of caudal furca enclosed in arch. Caudal rami (Fig. 19D, G) long, narrow, rhomboid with almost parallel sides (length

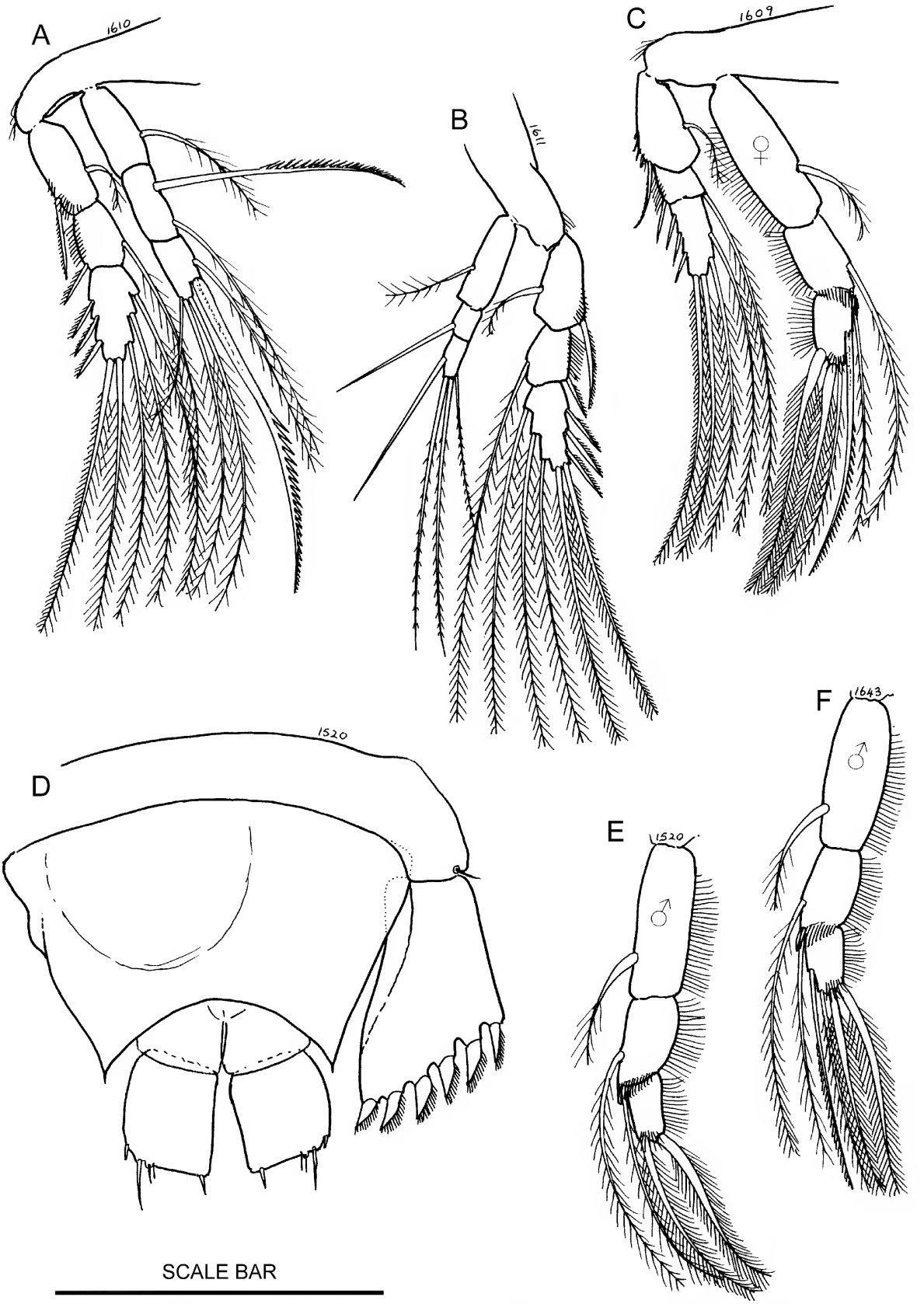

Figure 21. *Acutiramus bipunctatus* sp. nov. Female: *(A)* P3; *(B)* P4; *(C)* P2. Male: *(D)* genital double-somite and P5; *(E)* P2 endopod; *(F)* abnormal P2 endopod (see text). Scale bar: A–F = 0.13 mm.

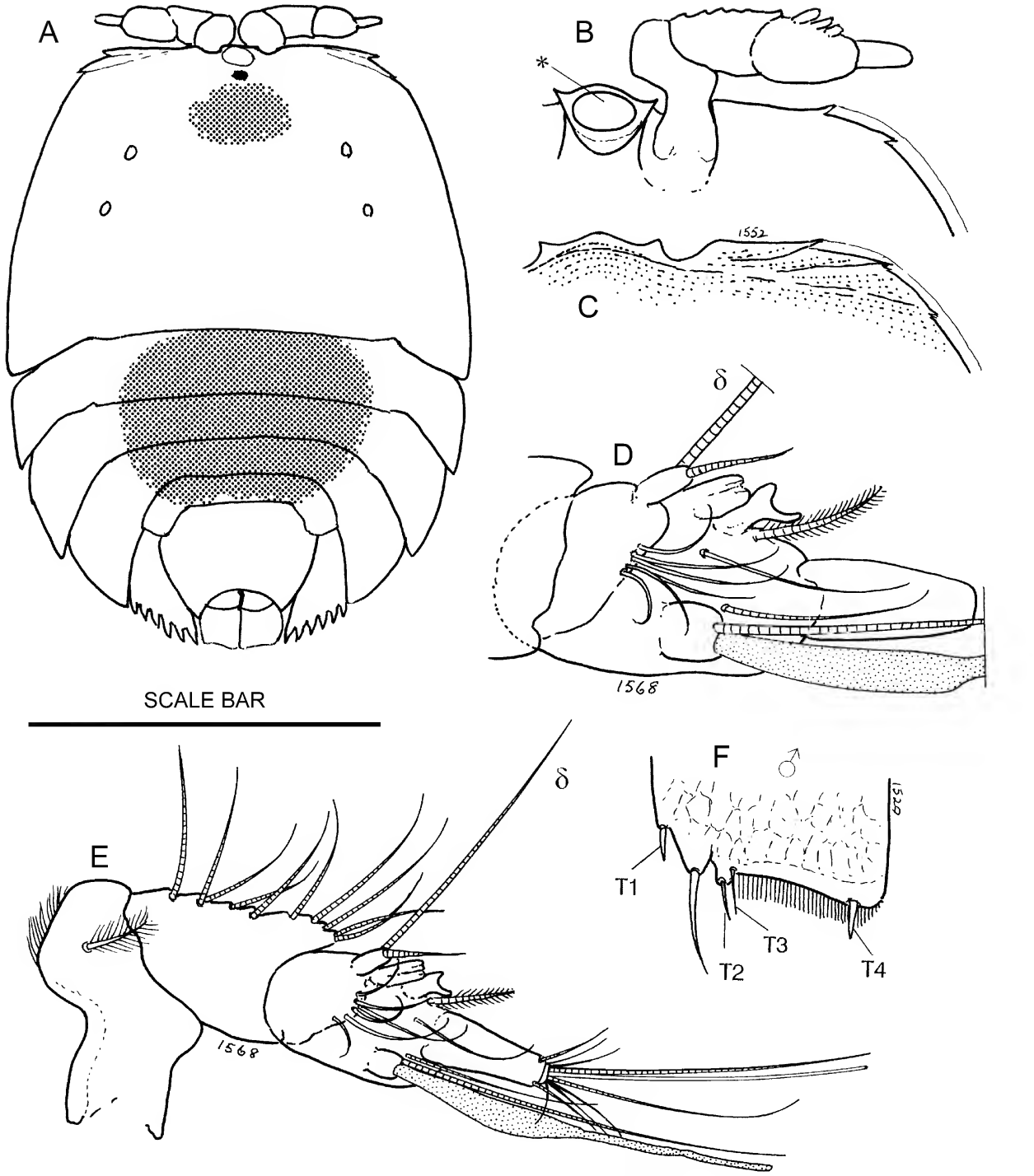

Figure 22. *Acutiramus bipunctatus* sp. nov. Male: *(A)* adult; *(B)* rostrum (ventral, * "lens"); *(C)* anterior cephalosome (dorsal); *(D, E)* antennule; *(F)* caudal ramus (detail). Scale bar: A = 0.34 mm. B, C = 0.15 mm. D, F = 0.06 mm. E = 0.08 mm.

3½ times width), medial and lateral edges without setules, dorsal surface with feint reticulation. α and β setae not close, β seta half way down ramus, terminal setae plain, T1 small, recessed at lateral corner, T2 small, T3 very small and delicate, T3 lies extremely close to T2 (on many specimens T2 and T3 appear to be absent, but this is probably due to the P5 limb rubbing against the posterior border of the caudal ramus and breaking off the setae), posterior border slightly concave with fine setules. No plumulose setae on antennule. Structure and setation of mouth parts and ambulatory limbs typical of family. Antenna exopod with five plumulose setae and one plumulose spinous seta (Fig. 20C), endopod segment 2 with three lateral setae, geniculate setae with plain terminal portion, comb-like claw ½ length of shortest geniculate seta. Mandible (Fig. 20A) without setules on anterior lobe of palp or molar process. Maxillule (Fig. 20D) with single seta on exopod. Maxilla (Fig. 20I) and maxilliped (Fig. 20B) as shown in figures. No area of denticulate setules on P1 endopod (Fig. 20G). Serrulate spinous seta on P2 endopod segment 3 shorter than endopod (0.8:1) (Fig. 21C).

Serrate spinous seta on P3 endopod segment 2 as long as endopod (Fig. 21A), large serrate spinous seta on segment 3 of endopod very long (1.5:1). Endopod of P3 and P4 with internal seta on segment 1, one plain spinous setae on P4 segment 2 and 3 (Fig. 21B). P5 exopod broad, truncated posteriorly, appears almost rectangular when laid flat, first dorsal seta small, two small apical setae, dorsal surface with pits (Fig. 20E). Females carry four or five very large eggs in brood chamber (eggs measure 0.1 × 0.06 when first laid).

Adult males (Fig. 22A), colouration same as female. Anterior outline of cephalosome a truncated semi-ellipse with small bulge above rostrum, shoulders rounded (Fig. 22C). Rostrum with conspicuous oval lens-like body just in front of eyespot seen from ventral view (Fig. 22B). Dorsal pits and hyaline border same as female. Caudal ramus (Fig. 19C) slightly longer than broad (1.15:1), lateral edge convex, posterior border between T2 and T4 slightly concave with border of fine setules, T4 set in from medial corner, T2 small, T3 very small, thin and very close to T2 (Fig. 22F). Antennule (Fig. 22E) with plumose seta on segment 1, no plumose setae on segment 2, no ventral process or blade, distal coupling denticle with C-shaped edge accompanied by a pinnate seta (Fig. 22D), dactylus elongate, cylindrical. Male P2 endopod (Fig. 21E) with two or four plumose setae (Fig. 21F, see Remarks below). Male P5 exopod trapezoid, no setules at base of terminal setae (Fig. 20F).

Etymology. The species name refers to the smaller red dot on the cephalosome and a larger red area on the metasome segments.

Remarks. The exopods of female P5 limbs wrap round and touch the bevelled edge of the caudal rami, consequently the delicate T2 and T3 setae are frequently broken off and not always seen. This gives the impression that T3 is missing in this species. Critical examination of recently metamorphosed females confirm that both T2 and T3 are present in this species.

During measurement of the eleven male animals it was noticed that seven specimens had two plumose terminal setae to segment 3 of P2 endopod, but four animals had four terminal setae (one serrulate spinous seta plus three plumose setae). Because four terminal setae is the normal condition for all female animals in the Porcellidiidae, this unusual observation probably indicates a case of paedomorphosis. The presence of four terminal setae on male P2 has only been recorded for two other species, *Dilatatiocauda tristanensis* (Wiborg, 1964) and *D. plana* (Tiemann, 1977), see Harris (2002).

Distribution. *Acutiramus bipunctatus* is abundant on *Halimedia* sp., *Zonaria* sp., and *Eucheuma* sp., at Point Vernon, Hervey Bay, Queensland, but it is also found in small numbers on *Caulerpa* sp., *Lethesia* and *Martensia* spp., in the same locality. The type series, PV6.7/97, contains 78 ♀♀ (70 with eggs), 41 ♂♂, 5 juveniles. Sample PV7. 8/97 from *Eucheuma denticulata* contains 407 ♀♀, 119 ♂♂ + 6 ♂♂ coupled with juvenile, V. A. Harris, 1997.

Acutiramus edenensis sp. nov.

Figs 23–25

Type material. HOLOTYPE adult male, length 0.48 mm, P81201; ALLOTYPE adult female, length 0.68 mm, P81202; PARATYPE material, 5 ♀♀, 3 ♂♂, 1 ♂ coupled to juvenile + 2 juveniles, P81203, deposited at AM, Sydney. Additional paratypes deposited at NHM, London. All collected from *Ecklonia radiata* at Arrawarra Headland, Woolgoolga, northern NSW (30°03'S 153°02'E), V. A. Harris, 1982.

Diagnosis. No plumose setae on segment 2 of male antennule, anterior lobe with δ on segment 3 long, finger-like, ventral blade absent, coupling denticles on segment 4 with serrated edge (Fig. 25G), dactylus broad with terminal claw-like hook and large lateral indentation (Fig. 25B, C); P3 endopod with internal seta on segment 1; rostrum prominent, without "lens", no median anterior bulge to cephalosome; male shoulders rounded, no epaulette; lateral edge of female caudal ramus slightly convex, posterior half of medial edge with setules, terminal setae plain, T1 as large as T4, T2 and T3 close together, not parallel to posterior edge, space between T3 and T4 about ⅓ length of oblique posterior edge, α and β not close (⅓ length of ramus apart); female P5 exopod truncated lanceolate; male spermatophore very small (< 15% of body length).

Biometric data. *Females* (N = 20): maximum length (L_{max}) mean 0.67 mm, range 0.63–0.72 mm, body length (L_{urs}) mean 0.64 mm, range 0.59–0.69 mm; cephalosome 0.42 mm, range 0.40–0.44 mm; rostrum width 0.115 mm; genital double-somite width 0.23 mm, length 0.16 mm, height of arch 0.09 mm; caudal ramus length 0.78 mm, width 0.28 mm.

Ratios: L_{urs}/W 1.52; W/R 3.5; genital double-somite w/l 1.47, arch 56% of somite length; caudal ramus 12% of body length (L_{urs}), caudal ramus l/w 2.8, Hicks index for β 53%.

Males (N = 15): maximum length (L_{max}) mean 0.49 mm, range 0.45–0.51 mm, body length (L_{urs}) mean 0.47 mm, range 0.44–0.49 mm; cephalosome width 0.35 mm; caudal ramus length 0.02 mm, width 0.018 mm; antennule fully extended 0.15 mm; spermatophore 0.06 mm × 0.018 mm.

Ratios: L_{urs}/W 1.35; caudal ramus l/w 1.1; antennule 32% of body length (L_{urs}), antennule segment 2 23%, segment 3+4 40%, dactylus 33% of antennule length; spermatophore 12% of body length (L_{urs}).

Description. *Adult females* (Fig. 23A): colourless, anterior outline of cephalosome semicircular, rostrum prominent, no median bulge above rostrum, no lens-like structure in rostrum. Dorsal pits small 2–3 µm, hyaline border granulated, 8–10 µm wide (Fig. 25E). Very few dorsal sensilla. Genital double-somite (Fig. 23F) almost semicircular in outline without anterolateral ridge, notch and short cleft mark boundary between anterior and posterior lobes, posterior lobe about 30% of lateral edge, arch of genital double-somite deep, accommodates more than ¾ of caudal furca. Genital opening as shown in Fig. 23E. Caudal ramus (Fig. 23B) rhomboid, length about 2½ times width, medial edge straight with fine setules from level of β to T4, lateral edge slightly convex with border setules distally, α and β setae not close,terminal setae plain, T2 and T3 very close together, space between T3 and T4 with fine setules, ⅓ length of oblique posterior edge, T4 inserted at rounded posterior apex. No plumulose setae on antennule. Structure

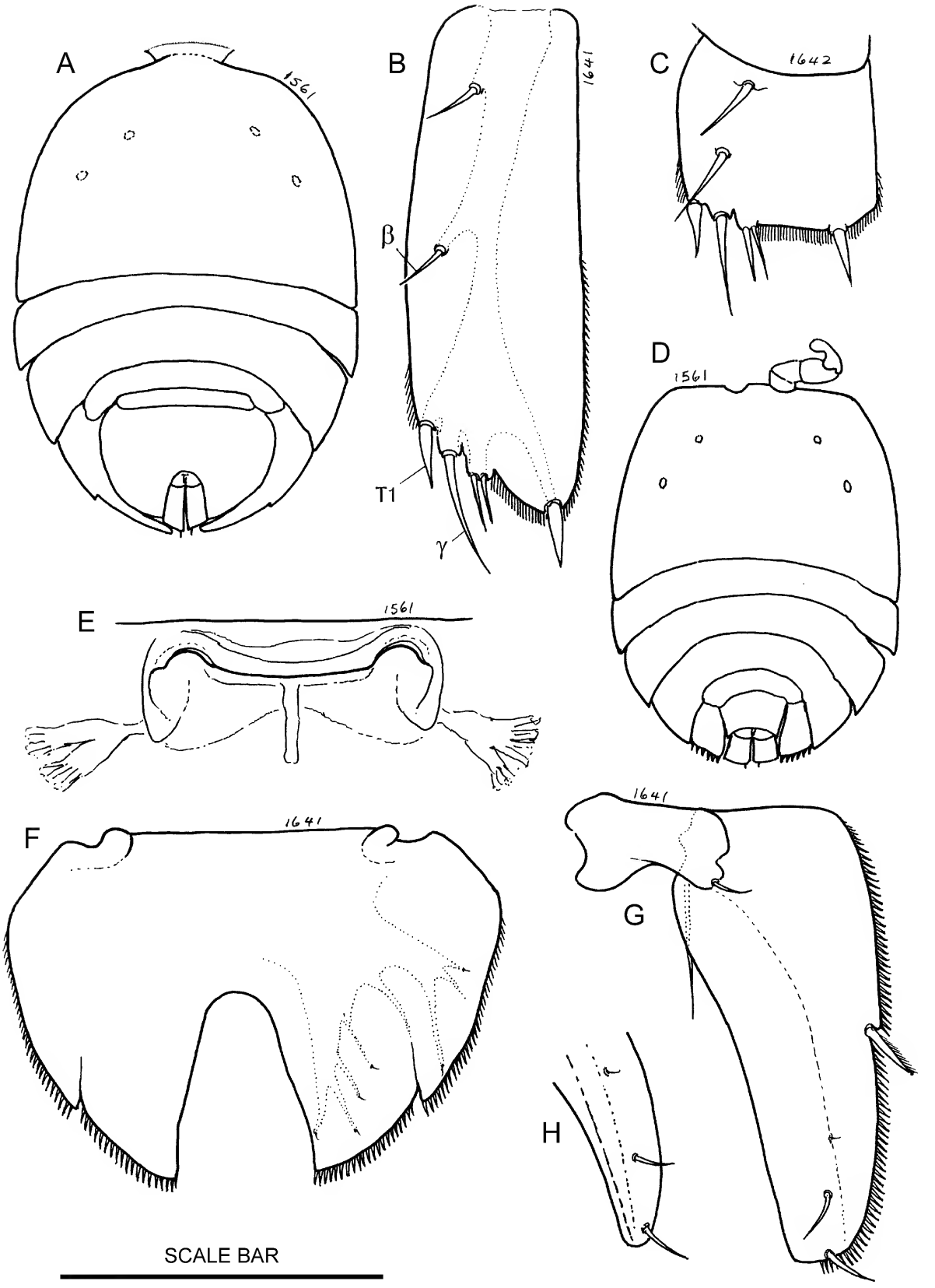

Figure 23. *Acutiramus edenensis*. sp. nov. Female: *(A)* adult; *(B)* caudal ramus; *(E)* genital opening; *(F)* genital double-somite; *(G, H)* P5 (dorsal). Male: *(C)* caudal ramus; *(D)* adult. Scale bar: A, D = 0.45 mm. B, C = 0.06 mm. E = 0.08 mm. F, G = 0.15 mm.

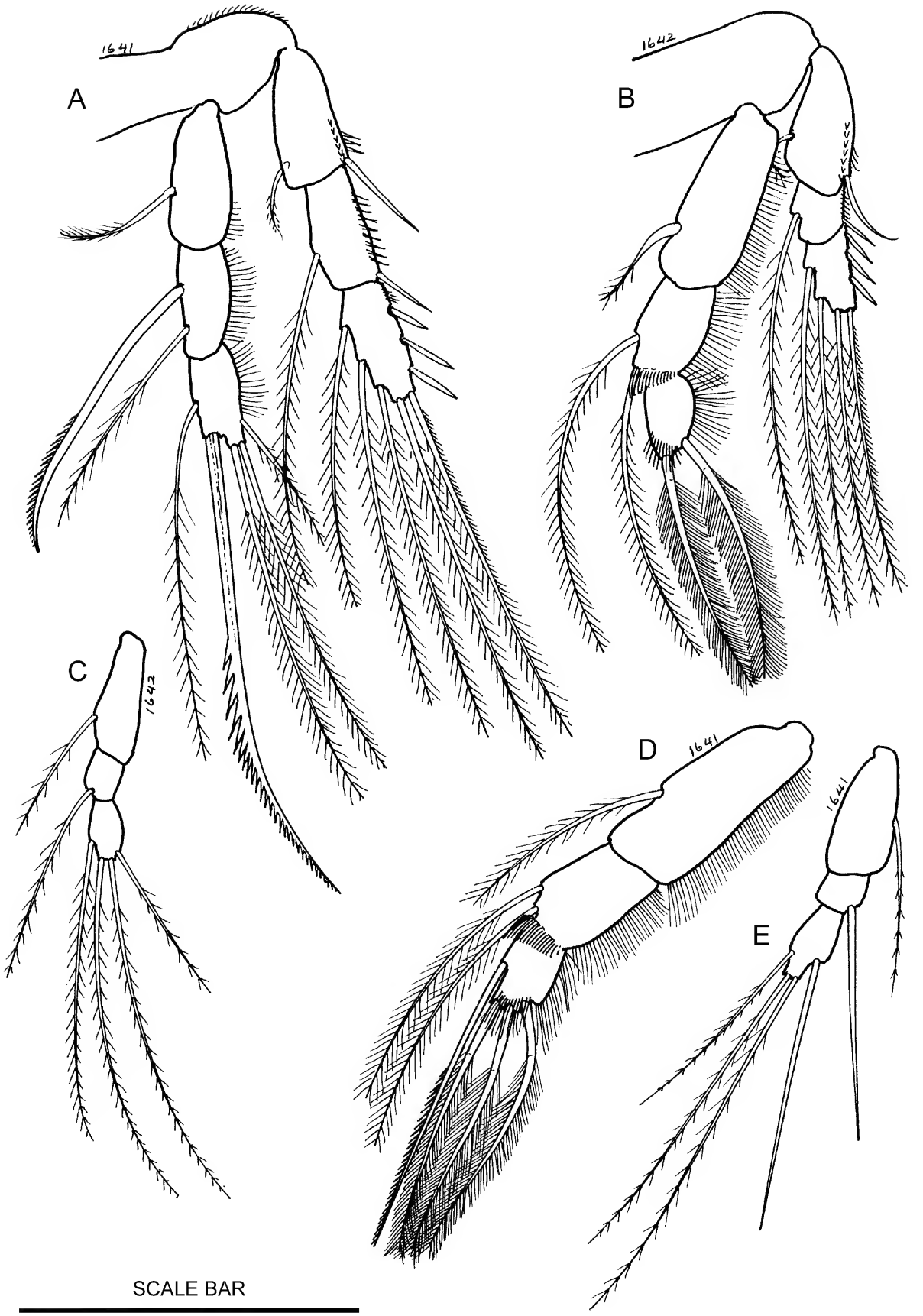

Figure 24. *Acutiramus edenensis* sp. nov. Female: *(A)* P3; *(D)* P2 endopod; *(E)* P4 endopod. Male: *(B)* P2; *(C)* P4 endopod. Scale bar: A–E = 0.1 mm.

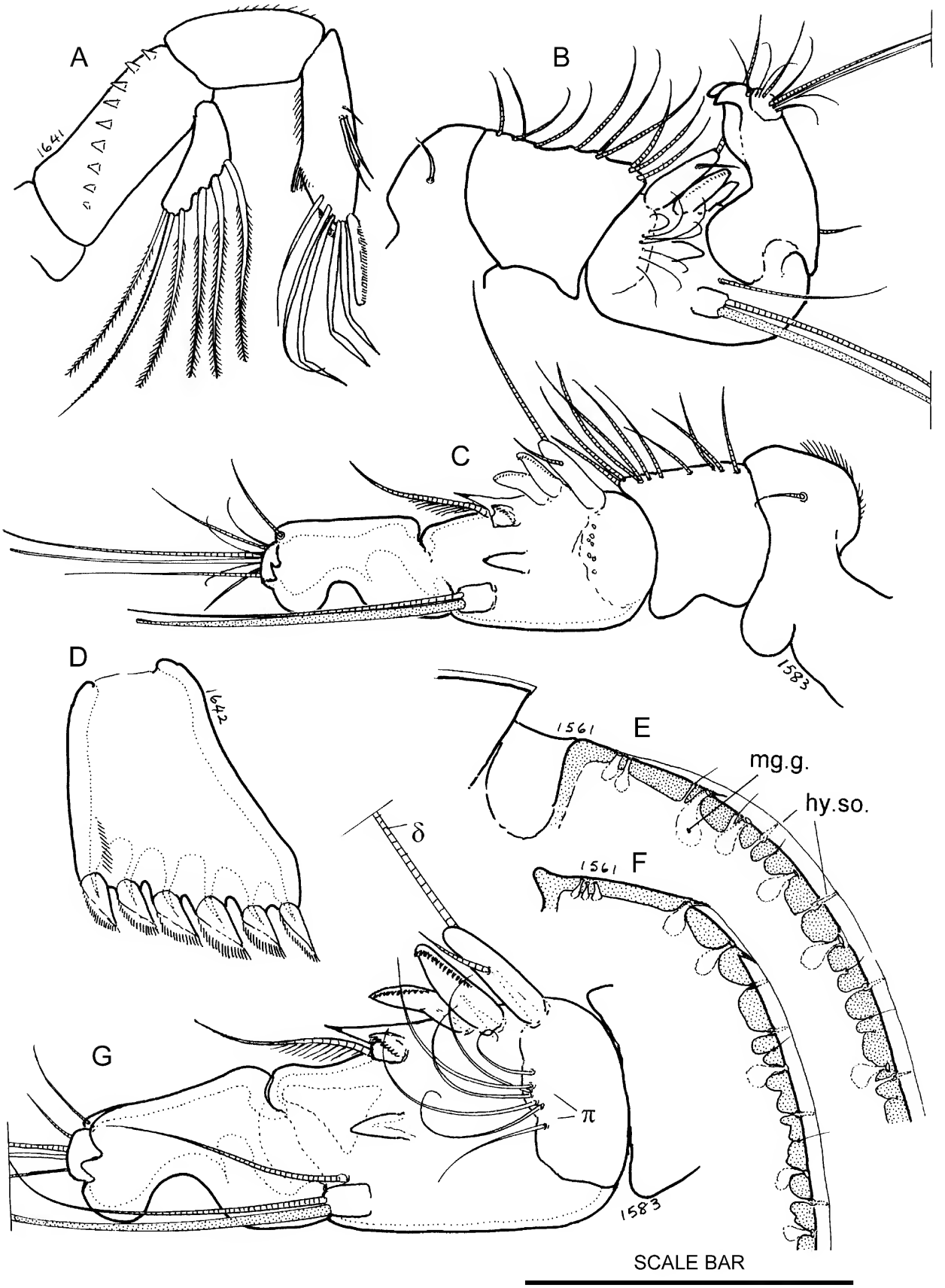

Figure 25. *Acutiramus edenensis* sp. nov. Female: *(A)* antenna; *(E)* border of cephalosome. Male: *(B, C, G)* antennule (π setae not shown in *C*); *(D)* P5 (ventral); *(F)* border of cephalosome. Scale bar: A, C, D = 0.08 mm. B = 0.13 mm. E, F = 0.15 mm. G = 0.06 mm.

Table 1. Difference in body size and number of eggs carried by the female in *A. edenensis* collected from northern New South Wales, Australia (latitude 30°S) and cooler temperate waters of southern NSW (latitude 37°S).

	Latitude 30°S N = 20	Latitude 37°S N = 26
L_{urs} mean	0.64 mm, range 0.59–0.69 mm	0.75 mm, range 0.72–0.81 mm
W mean	0.42 mm, range 0.40–0.45 mm	0.50 mm, range 0.45–0.53 mm
R mean	0.115 mm	0.135 mm
	Ratios	
L_{urs}/W	1.5	1.53
W/R	3.7	3.65
Number of eggs	mean 5, range 4–6	mean 8, range 6–12

and setation of mouth parts and ambulatory limbs typical of family. Antenna (Fig. 25A) with row of triangular setules on basis, five plumulose setae plus one finely serrulate spinous seta on exopod, segment 2 of endopod with three lateral setae, end part of geniculate setae plain, terminal claw comb-like, long. Mandibular palp without setules on anterior lobe. Maxillule, maxilla and maxilliped as described for *A. bipunctatus*. No peg area on P1 endopod. Serrulate spinous seta on segment 3 of P2 endopod shorter than endopod (0.75:1) (Fig. 24D). P3 with internal seta on segment 1 of endopod, serrulate spinous seta on segment 2 of P3 endopod (Fig. 24A) shorter than endopod, large serrate spinous seta on segment 3 longer than endopod (1.37:1).Endopod of P4 with internal seta on first segment, plain spinous seta on segment 2 and first (internal) seta of segment 3 (Fig. 24E). Exopod of P5 lanceolate, truncated posteriorly, two dorsal setae, one very small and one larger sub-terminal, one apical seta, dorsal surface with pits (Figs 23G, H). See Remarks for number of eggs carried by the female.

Adult males (Fig. 23D) colourless. Anterior of cephalosome truncated semi-ellipse, no medial bulge above rostrum or lens-like body in rostrum, shoulders rounded. Caudal ramus (Fig. 23C) quadrate, medial edge straight, lateral edge slightly convex, T2 and T3 very close, T4 set in from medial corner, terminal fringe of fine setules. Antennule (Figs 25C), no plumose setae on segment 2, anterior lobe on segment 3 extended as long finger-like process bearing δ and δ' setae, no ventral process or blade on segment 3, two elongate coupling denticles with comb-like edge on segment 4 project forward parallel to anterior lobe, distal denticle small with pinnate seta, small pointed structure in "palm" of segment 4 (Fig. 25G), dactylus almost as long as segment 3+4 with characteristic deep indentation on its posterior edge, hooked terminally (Figs 25B, G). Endopod of P2 with two plumose setae on terminal segment (Fig. 24B). All setae on P4 endopod plumose, not spinous (Fig. 24C). P5 trapezoid, no setules at base of terminal setae except first or lateral seta (Fig. 25D). Spermatophore extremely small (about 12% of body length).

Etymology. The specific name refers to Eden NSW where the species was first discovered.

Remarks. A difference in body size and number of eggs carried by the female has been noticed between animals collected from northern NSW and those found in cooler temperate waters of southern NSW (Table 1).

Distribution. *Acutiramus edenensis* has a wide geographical range covering more than 7° of latitude. The type series was collected from mixed seaweeds (including *Ecklonia radiata*) in the infralittoral fringe, Woolgoolga (30°03'S), Wo3. 11/82, 35 ♀♀ (19 ovigerous), 17 ♂♂ plus 4 ♂♂ coupled to juveniles, 13 juveniles. It has been found at Broulee, NSW, (35°52'S) on *Caulerpa* sp., and in washings from *Ecklonia radiata* holdfasts at Twofold Bay, Eden, NSW, (37°06'S), TB4. 12/82, 11 ♀♀, 3 ♂♂, V. A. Harris 1982.

Acutiramus iwasakii sp. nov.

Figs 26, 28, 29

Type material. HOLOTYPE adult male, length 0.54 mm, mounted on slide [1360], P88555; ALLOTYPE adult female without egg mass, length 0.70 mm, mounted on slide [939], P88556 deposited at AM, Sydney; additional PARATYPES deposited at NHM, London. All collected from inside *Turbo torquatus* shells inhabited by hermit crabs of the species *Pagurus sinuatus*, O'Hara Head, Kioloa, NSW (25°34'S 150°25'E, estimated), V. A. Harris, 1976.

Diagnosis. Female rostrum unique, anterior edge with three curves giving an undulating appearance (Fig. 26D), hyaline border present; male rostrum with anterior point, not obscured by cephalosome above; setae on male antennule sensory lobe and dactylus extremely long (> than length of antennule); female caudal ramus rhomboid with pinnate T4 at posterior apex, setules down length of medial edge, gap between γ and T2 equals gap between T3 and T4, α and β setae close (⅙ of ramus length apart); seta T1 on male caudal ramus very small; female genital double-somite with short cleft between anterior and posterior lobes; P3 endopod without seta on segment 1 (0:2:1, 3, 1); P4 endopod without seta on segment 1 (0:1:1, 2, 1).

Biometric data. *Females* (N = 6): maximum length (L_{max}) mean 0.72 mm, length to posterior of genital double-somite (L_{urs}) mean 0.66 mm; width of cephalosome (W) 0.50 mm; rostrum width (R) 0.10 mm; genital double-somite length 0.13 mm, width 0.22 mm, arch 0.09 mm; caudal ramus length 0.08 mm, width 0.04 mm.

Ratios: L_{max}/W 1.45, L_{urs}/W 1.35; cephalosome W/R 5.0; genital double-somite width 44% of cephalosome width, w/l 1.7, arch/l 0.7; caudal ramus l/w 2.0, ramus as % of L_{max} 13%, Hicks' index for α 83%, β 67%, α–β17%.

Males (N = 4): maximum length 0.54 mm; cephalosome width 0.40 mm; antennule 0.126 mm; angle of P5 apex 45°.

Ratios: Caudal ramus l/w 0.78, Hicks' index for α 60%, β 50%, α–β 11%; antennule 23% of L_{max}, segment 3+4 43%, dactylus 16% of antennule length.

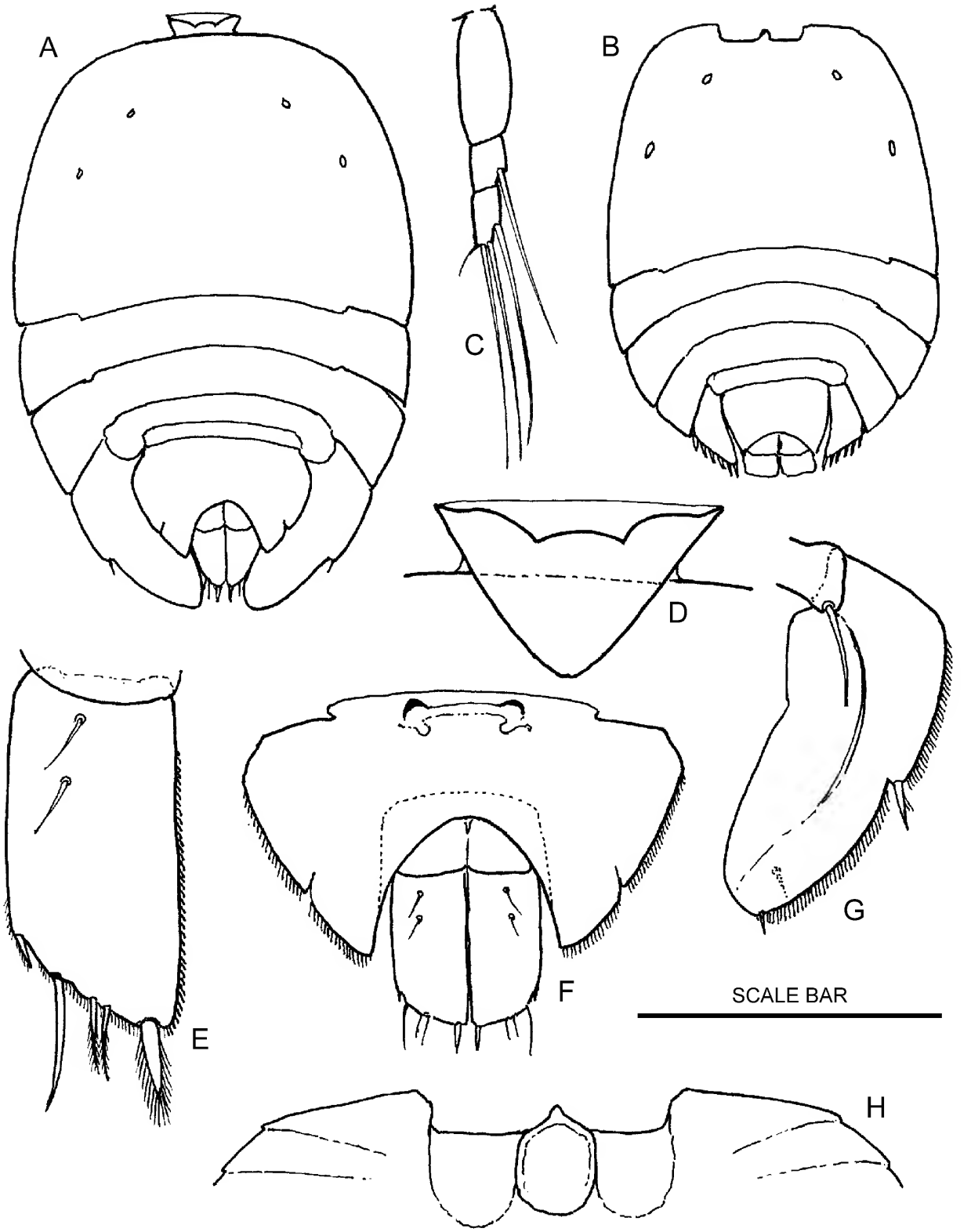

Figure 26. *Acutiramus iwasakii* sp. nov. Female: *(A)* adult; *(C)* P4 endopod; *(D)* rostrum (ventral); *(E)* left caudal ramus; *(F)* genital double-somite; *(G)* P5 ventral. Male: *(B)* adult; *(H)* anterior cephalosome (ventral showing rostrum). Scale bar: A, B = 0.36 mm. D = 0.12 mm. E = 0.07 mm. F, G, H = 0.16 mm.

Description. *Adult females* (Fig. 26A): colourless, transparent. Anterior of cephalosome semicircular, no bulge above rostrum. Rostrum prominent, with characteristic undulating anterior border (Fig. 26D). Dorsal pits small (3–4 µm), hyaline border 8 µm, dorsal surface without hair-like sensilla. Genital double-somite narrow, pointed posteriorly with a distinct cleft separating anterior and posterior lobes, border setules present, arch encloses about ½ of caudal ramus

(Fig. 26F). Caudal ramus (Fig. 26E) rhomboid with pinnate T4 at apex, medial edge with setules, α and β setae not very close, T1 very small at lateral end of bevelled posterior edge, T2 and T3 close, equally spaced between γ and T4, setules along bevelled edge. No setules on labrum. Structure and setation of mouthparts and ambulatory limbs are typical of family. Geniculate setae on segment 2 of antenna endopod with plain terminal segment, terminal claw not comb-like, as long as first geniculate seta (Fig. 29A). Maxillule (Fig. 29C), P3 does not have internal seta on segment 1 of endopod (0:2:1,3,1). The serrate spinous terminal seta on P3 endopod is slender and not much longer than the endopod (1.2:1). No internal seta on segment 1 of P4 (0:1:1,2,1), (Fig. 26C). P5 is broad and partly covers the genital double-somite, it is rounded posteriorly with an apical seta and one sub-terminal dorsal seta (Fig. 26G). Mature females carry four or five large eggs.

Adult males (Fig. 26B) colourless. Anterior of cephalosome only slightly truncated, shoulders rounded bearing two rows of dorsal pits arranged along a ridge (Fig. 29D). The rostrum has a prominent anterior point that is not obscured dorsally. The rostrum and antennule sockets are recessed in a medial anterior concavity of the cephalosome (Fig. 26H). Dorsal pits and hyaline border as for female. Caudal ramus sub-quadrate (l/w = 0.8), α and β setae close together (⅒ of ramus length), terminal setae appear to be plain, T1 is very short, recessed, T2 and T3 close, gap between T3 and T4 is ⅓–½ width of ramus (Fig. 28B). Antennule is unique for the length of its setae (Fig. 28G). Both the terminal seta on dactylus and σ seta on sensory lobe are as long, or longer, than length of extended antennule, δ seta ⅔ length of antennule, annulate seta associated with the distal denticle is equal to segment 3+4 in length. No denticle on segment 3, two denticles on segment 4 (Fig. 28F). Structure and setation of mouthparts and ambulatory limbs as for female, but P2 has two terminal setae on segment 3 of the endopod, P5 acute trapezoid (Fig. 28D), no rows of setules at base of each terminal seta.

Etymology. The species has been named after Dr Nozomu Iwasaki in recognition of his studies on *Dactylopusoides* species that burrow into brown algae.

Remarks. Nearly all animals in the present study are heavily burdened with protozoan organisms (large thecate and small naked suctoria as well as other thecate protozoa) which obscure detail of important organs such as the caudal rami and male antennules (see Fig. 27A). For this reason it was necessary to base identification and description on three newly metamorphosed specimens that had not been colonized by protozoa.

Animals were found living inside the shells occupied by the hermit crab *Pagurus sinuatus*, but not on empty shells or those occupied by the mollusc, thus the relationship appears to be commensal.

Acutiramus cumulus sp. nov.

Figs 27–29

Type material. HOLOTYPE adult male, length 0.55 mm, dissected, P89051, and ALLOTYPE, adult female not carrying eggs, length 0.78 mm, both mounted on a slide [1651], P89052, deposited at AM, Sydney. Additional PARATYPES deposited at NHM, London. All collected from inside *Turbo torquatus* shells inhabited by hermit crabs of the species *Pagurus sinuatus*, O'Hara Head, Kioloa, NSW, (25°34'S 150°25'E, estimated), V. A. Harris, 1976.

Diagnosis. Male rostrum without anterior point, anterior border of cephalosome convex in midline obscuring rostrum, slightly concave on each side with angular shoulders; T1 on male caudal ramus large, pinnate, α and β setae not close together (¼ length of ramus apart); anterior border of female rostrum straight, cephalosome bulged above rostrum; female caudal ramus rhomboid with conspicuous network of ridges; terminal setae T2, T3 and T4 pinnate, equal in size and bunched up together at posterior apex; no internal seta on segment 1 of P3 endopod (0:2:1,3,1); P4 has plain internal seta on segment 1 of endopod (1:1:1,2,1); setae on male antennule not longer than antennule (< ½ antennule length).

Biometric data. *Females* (N = 8): maximum length (L_{max}) mean 0.78 mm, length to posterior of genital double-somite (L_{urs}) mean 0.72 mm; width of cephalosome (W) 0.51 mm; rostrum width (R) 0.12 mm; genital double-somite length 0.16 mm, width 0.26 mm, arch 0.09 mm; caudal ramus length 0.10 mm, width 0.03 mm.

Ratios: L_{max}/W 1.5, L_{urs}/W 1.4; cephalosome W/R 4.2; genital double- somite width 50% of cephalosome width, w/l 1.65, arch/l 0.55; caudal ramus l/w 3.1, ramus as % of L_{urs} 14%, Hicks' ratios α 88%, β 61%, α–β 27%.

Males (N = 2): maximum length 0.58 mm; cephalosome width 0.42 mm.

Ratios: Caudal ramus l/w 1.0, Hicks' index for α = 70%, β 42%, α–β 28%.

Description. *Adult females* (Fig. 27A): colourless, anterior of cephalosome semicircular with a distinct bulge above the rostrum. Rostrum prominent with slightly convex anterior border (Fig. 27G). Dorsal surface without hair-like sensilla, dorsal pits large (6–9 μm) conspicuous over all parts of the body except the caudal rami. Genital double-somite posterior lobe pointed, separated from anterior lobe by a distinct cleft (Fig. 27B). Caudal ramus (Fig. 27F) rhomboid, long (length 2½ times width) with conspicuous dorsal network of ridges, α and β setae not close (> ¼ length of ramus). The arrangement of terminal setae is unique, T2, T3 and T4 are clustered together at the posterior apex of the ramus (Fig. 27F), T1 is small at the lateral end of the bevelled posterior edge and there is a gap between γ and T2. A terminal fringe of setules could not be seen on specimens available. Labrum without setules. Structure and setation of mouthparts and ambulatory limbs typical of family except for P3 which lacks internal seta on segment 1 of endopod. Serrated spinous seta on segment 3 of P3 much longer than endopod (1.6:1). P4 endopod (Fig. 27C) has plain internal seta on segment 1, P5 broad, rounded posteriorly with apical seta and one sub-terminal seta (Fig. 27D). Mature females carry four or five large eggs.

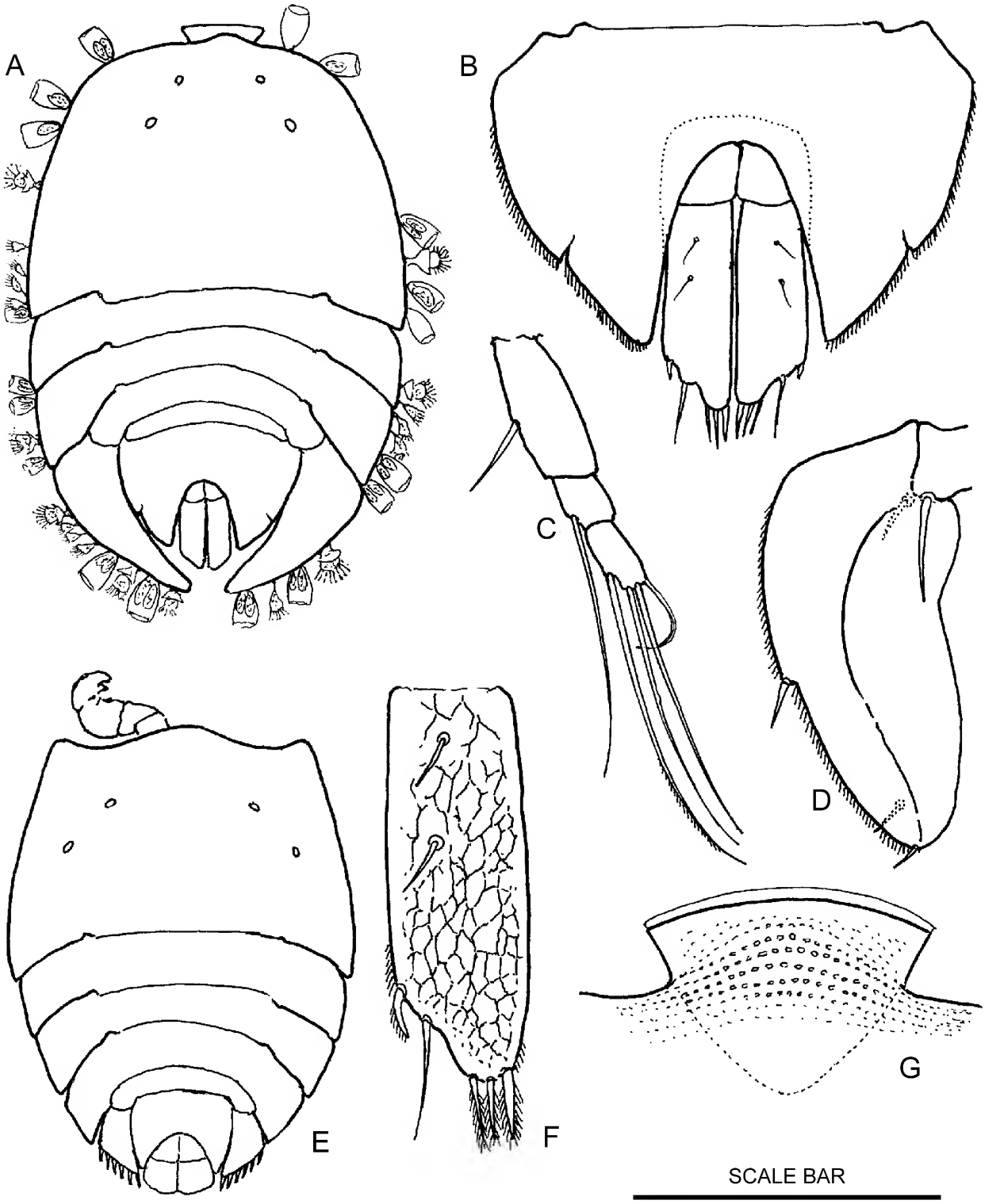

Figure 27. *Acutiramus cumulus* sp. nov. Female: *(A)* adult (with attached protozoa); *(B)* genital double-somite; *(C)* P4 endopod; *(D)* P5 (ventral); *(F)* left caudal ramus; *(G)* rostrum. Male: *(E)* adult. Scale bar: A = 0.42 mm. B, D = 0.16 mm. E = 0.38 mm. F = 0.07 mm. G = 0.13 mm.

Adult males (Fig. 27E) colourless. Anterior of cephalosome truncated, convex in midline above the rostrum and slightly concave on either side with pointed shoulders. Rostrum not pointed, obscured from above by cephalosome (Fig. 28A). Dorsal pits as for female. Caudal ramus (Fig. 28E) quadrate, lateral edge convex, dorsal surface with rows of conspicuous pits, α and β setae not close (¼ length of ramus apart). Terminal seta T1 pinnate, recessed at lateral corner, T2 and T3 pinnate close together in middle of posterior border, T4 small set in from rounded medial corner. Antennule (Fig. 29B) sensory lobe on segment 4 does not have a blade-like (acuminate) process, all setae less than

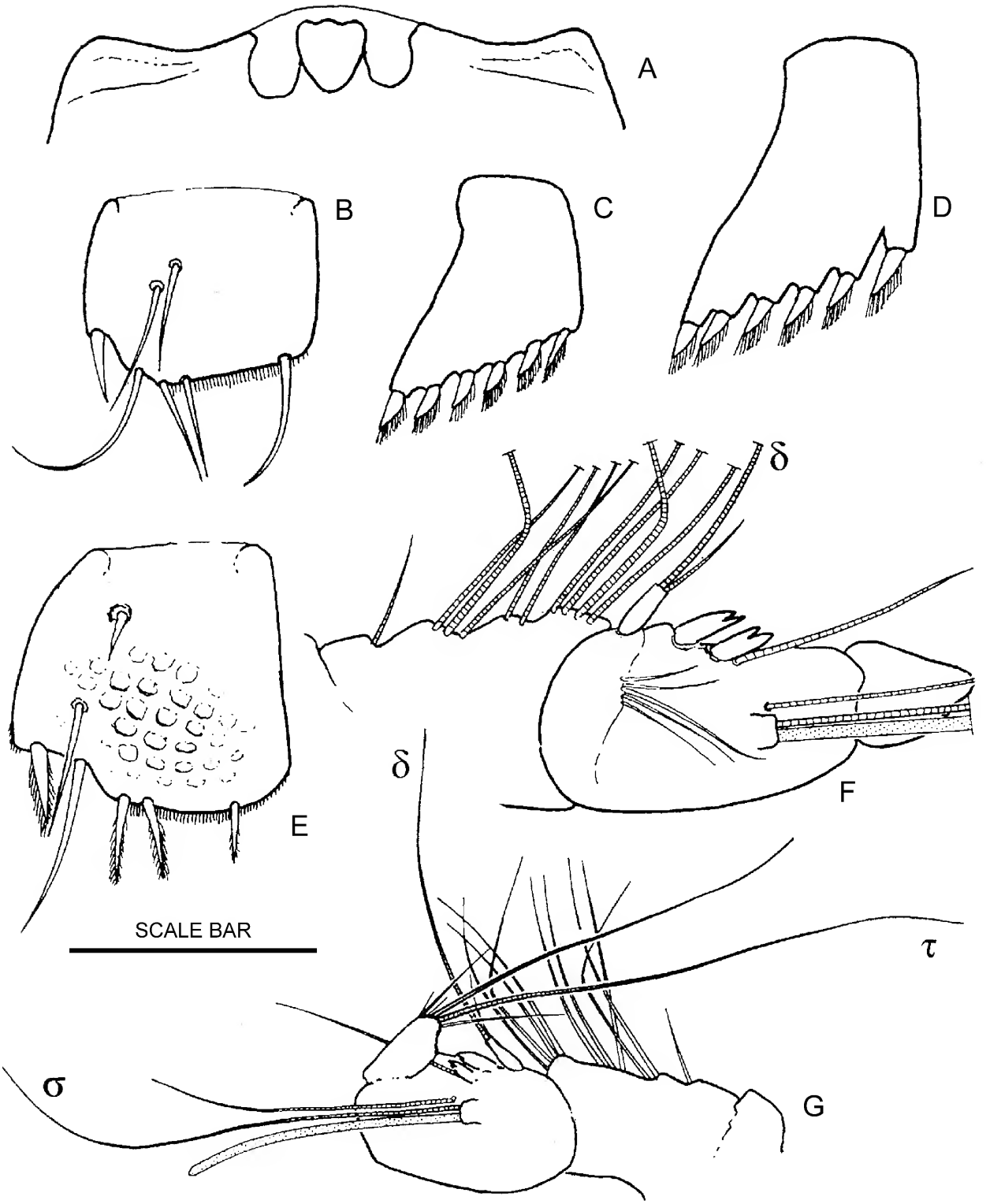

Figure 28. *Acutiramus cumulus* sp. nov. male: *(A)* anterior cephalosome (ventral, showing rostrum); *(C)* P5; *(E)* left caudal ramus. *Acutiramus iwasakii* sp. nov. male: *(B)* left caudal ramus; *(D)* P5; *(F)* antennule denticles; *(G)* antennule setae (π series not shown). Scale bar: A = 0.2 mm. B = 0.04 mm. C, D, G = 0.065 mm. E, F = 0.04 mm.

length of antennule. (No fully extended antennule available for measurement and study of denticles). Structure and setation of mouthparts and ambulatory limbs as for female. P2 has two terminal setae on segment 3 of the endopod, P5 is trapezoidal with apical angle 47° (Fig. 28C) no rows of setules at base of terminal setae.

Remarks. The trivial name refers to the way in which terminal setae T2, T3 and T4 on the female caudal ramus are heaped together at the apex (L. *cumulus* = a heap or pile), this feature has not been found on any other member of the family.

Specimens of *A. cumulus* and *A. iwasakii* were found living together in the same shells inhabited by hermit crabs.

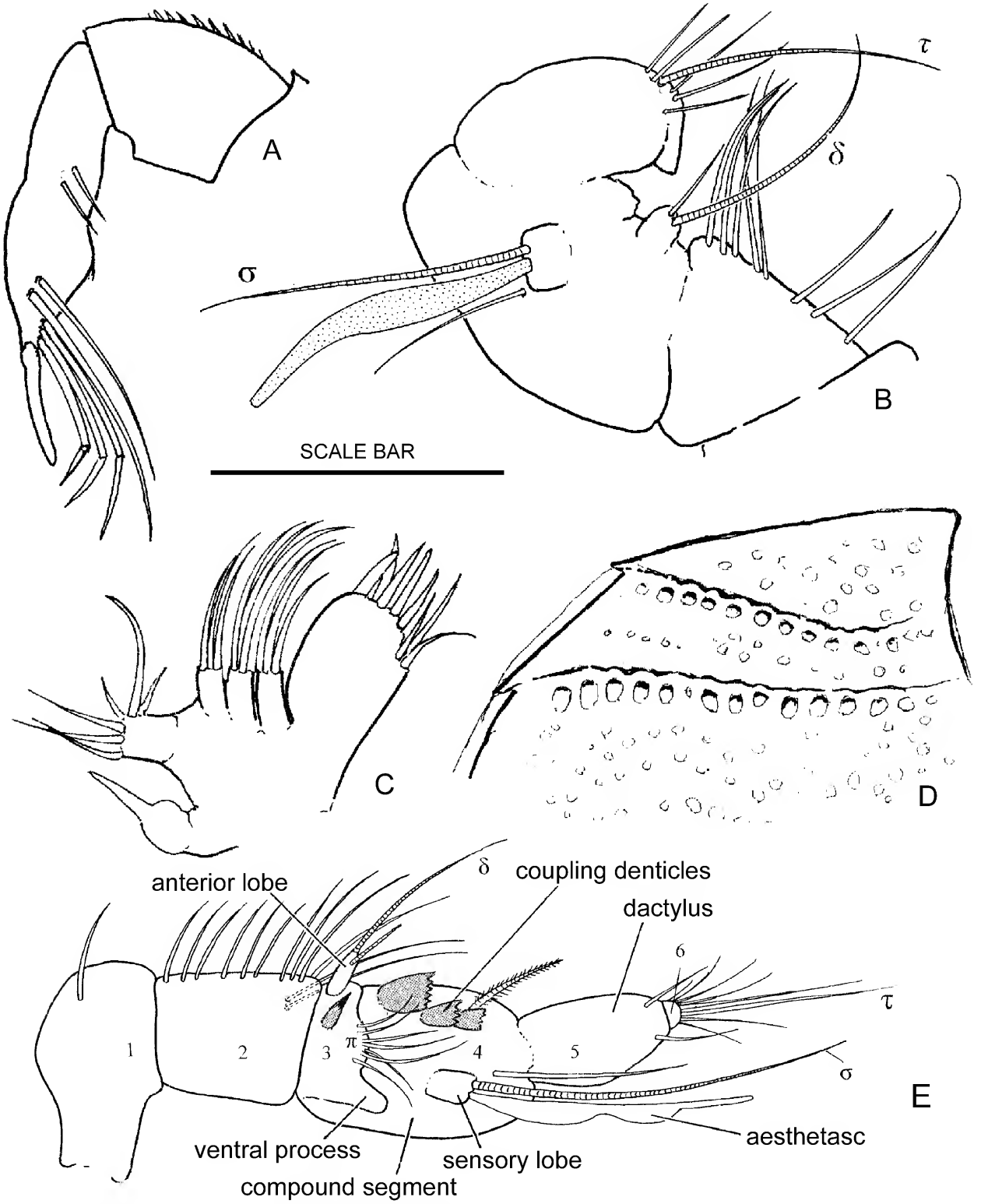

Figure 29. *Acutiramus iwasakii* sp. nov. Male: *(A)* antenna endopod; *(C)* maxillule; *(D)* ridges and pits on left shoulder. *Acutiramus cumulus* sp. nov. male: *(B)* antennule setae; *(E)* diagram showing terminology used in description of male antennule. Scale bar: A, B, C = 0.05 mm. D = 0.06 mm.

Both species are heavily burdened with suctorian protozoans round their perimeter (compare with Fig, 28A).

Porcellidium tapui described by Hicks & Webber, 1983 does not fit the diagnosis for *Porcellidium*, but fits the diagnosis for *Acutiramus* and should be moved to that genus as *A. tapui* (Hicks & Webber, 1983). *A. tapui* displays a degree of variability in morphology and measurements that is unknown among algal living species, Hicks & Webber (1983). The question arises whether *A. cumulus* may be just an extreme form of *A. tapui.* There are some similarities between the two animals, but there are also significant differences as shown in Table 2.

Table 2. Differences between Australian and New Zealand animals.

	Acutiramus cumulus	*Acutiramus tapui*
Females ♀♀		
1	Total length 0.78 mm.	Total length 0.69 mm.
2	Conspicuous bulge above rostrum.	Not mentioned.
3	Metasome segment 3 with reduced epimeral lobe that partly covers baseoendopod of P5.	Reduced epimeral lobe not shown, baseoendopod of P5 fully exposed.
4	Border setules on genital double-somite short, all same length.	Border setules of posterior lobe very long (three times longer than on anterior lobe).
5	Caudal ramus rhomboid (parallel sides).	Caudal ramus "sub-rectangular", tapers posteriorly.
6	T1 and γ setae deeply recessed.	T1 and γ only slightly recessed.
7	T2, T3 and T4 bunched together at apex. across medial half of posterior edge.	T2, T3, and T4 not bunched together, spaced evenly
8	α and β setae wide apart (27% of ramus length).	α and β setae closer together (17% of ramus length).
9	Dorsal surface of ramus covered with conspicuous ridges.	Reticulate pattern only recorded on distal part of ramus at 3 sampling locations.
10	Seta on segment 1 of P4 endopod plain.	Seta on segment 1 of P4 plumose.
Males ♂♂		
11	Sensory lobe of male antennule without blade-like appendage.	Blade-like (acuminate) appendage present on sensory lobe (morph 1).
12	Truncated anterior border of male cephalosome broad with angular shoulders and bulge in midline.	Anterior border not as broad, without angular shoulders.
13	α and β setae on male caudal ramus not close (28% of caudal length apart).	α and β setae on male caudal ramus close (20% of ramus length apart).
14	α and β setae on male caudal ramus short (length < ½ width of ramus).	α and β setae on male caudal ramus long (α and β setae ≥ than width of ramus).
15	Male T1 and γ setae recessed from posterior border.	Male T1 and γ not recessed.
16	Male P5 trapezoid, apical angle 47°	Male P5 "sub-rectangular", apical angle 60°

Note. It is considered that these differences justify naming the Australian and New Zealand animals as distinct species.

Genus *Clavigofera* Harris & Iwasaki, 1996

Clavigofera Harris & Iwasaki, 1996: 200.—Bodin, 1997: 67; Walker-Smith, 2001: 655; Wells, 2007:80.
Porcellidium.—Pesta, 1935: 377; Lang, 1948: 425; Humes & Gelerman, 1962: 311; Wells, 1967; Marques, 1977: 1057; Hicks, 1982: 64.

Type species. *Clavigofera pacifica* Harris & Iwasaki, 1996: 201–204, figs. 1–2.

Diagnosis. Male antennule without denticle on segment 3, segment 4 with two denticles (never brush-pad or denticulate pad), segment 6 distinct (not fused with segment 5); anterior lobe of female genital double-somite with lateral striations (rugosities) on ventral surface (Fig. 30B); female caudal ramus rectangular, widens slightly posteriorly, terminal setae large, pinnately clavate, evenly spaced across posterior border (Fig. 30C), T1 same size and shape as T2–T4, not recessed; cephalosome with hyaline border, marginal glands open dorsal to border, cuticular honeycomb absent; female genital double-somite narrow, pointed posteriorly; maxillule endopod with six setae; coxal lobes of maxillipeds touch in midline, basis with fimbriate process; no ventral expansion to female P5 exopod, P5s extend to or beyond posterior extremity of genital double-somite, do not touch posteriorly; male P5 trapezoid with one lateral and five terminal setae; spermatophore elongate, ephemeral on female.

Species composition. *Clavigofera clavigera* (Pesta, 1935); *C. echinophila* (Humes & Gelerman, 1962); *C. laurencia* (Hicks, 1982); *C. ulva* (Hicks, 1982); *C. pacifica* Harris & Iwasaki, 1996.

The genus is widely distributed and occurs in the southern Atlantic Ocean (St. Helena), Indian Ocean (South Africa, Mozambique, and Madagascar), northern Pacific Ocean (Japan, Hawaii) and southern Pacific Ocean (Australia).

Table 3. Values of Hicks' index for α seta on caudal ramus of *Cladofera* species.

species	α% (mean)	range (%)	number in sample	locality
Clavigofera pacifica	52.3	50–55.5	27	Iwate Prefecture, Japan
C. pacifica	52.7	51–55	23	NSW, Australia
C. echinophila *	52.3	49.5–55.5	8	Madagascar
C. laurencia *	57.6	56.3–60	10	South Africa
C. ulva *	62.5	59–65.5	10	South Africa
C. clavigera *	67.35	—	1	Hawaii

* data from Hicks (1982).

Key to the species of *Clavigofera*

1 δ seta on male antennule "whip-like" (> than length of antennule), length of female > 0.75 mm ..... *Clavigofera ulva* (Hicks, 1982)

—— δ seta on male antennule not long (< length of antennule). Length of female < 0.75 mm 2

2 Length of female ≤ 0.5 mm, Hicks' index for α seta > 65% ..... *Clavigofera clavigera* (Pesta, 1935)

—— Length of female > 0.5 mm, but < 0.75 mm, Hicks' index for α seta < 60% 3

3 α, β and γ setae of male = ¾ length of caudal ramus. Animals associated with sea urchins ..... *Clavigofera echinophila* (Humes & Gelerman, 1962)

—— α, β and γ setae less than ⅔ length of male caudal ramus. Animals found on seaweed 4

4 Hicks' index for α seta on female caudal ramus > 55%. Length of striated area < ¼ length of genital double-somite ..... *Clavigofera laurencia* (Hicks, 1982)

—— Hicks' index for α seta on female caudal ramus < 55%. Length of striated area = ⅓ length of genital double-somite ..... *Clavigofera pacifica* Harris & Iwasaki, 1996

Remarks. *Clavigofera pacifica* was first described from Iwate Prefecture, Honshu, Japan, Harris & Iwasaki (1996). Hicks (1982) placed emphasis on the position of the α seta on the female caudal ramus to separate species from S. Africa, Madagascar and Hawaii in his "*clavigerum* complex" (see Table 3 above). Harris & Iwasaki (1996) raised the "*clavigerum* complex" to generic status on the grounds that the striations on the genital double-segment and shape of the terminal setae on the caudal rami are apomorphic characters. Although the species look very similar, biometric differences support their separation into distinct species.

Based on ecological differences, statistical analysis of size and position of the α seta, Hicks (1982) considered *C. echinophila, C. laurencia* and *C. Ulva* to be three distinct species. Corresponding analysis shows that there is a highly significant difference in size and position of the α seta between *C. laurencia* and *C. pacifica. Clavigofera echinophila,* however, has the same value for α seta as *C. pacifica,* but morphological and ecological differences clearly show the two species are distinct, (*C. pacifica* lives on seaweed, *C. echinophila* lives in association with a sea urchin, Humes & Gelerman (1962).

Etymology. Pesta (1935) described the terminal setae on the caudal rami as "club-shaped" (keulenförmiger Gestalt). The generic name is derived from this, (L. *clava* = club + *fero* = to bear, carry).

Clavigofera pacifica Harris & Iwasaki, 1996

Figs 30–33

Clavigofera pacifica Harris & Iwasaki, 1996: 201, 204, figs. 1, 2.—Bodin, 1997: 67; Wells, 2007: 80.

Type material. Type locality: Kadonohama Bay, Ofunato, Iwate Prefecture, Japan. Holotype (female) NSMT-Cr 11950, allotype NSMT-Cr 11951 deposited in the National Museum of Natural Sciences, Tokyo, Japan.

Australian specimens from NSW deposited at the AM, Sydney, P89053, 20 ♀♀, 10 ♂♂, 8 ♂♂ coupled with juvenile female *ex Lobophora variegata*, Shelly Beach, Cronulla, Sydney, 34°03'S 151°11'E) V. A. Harris, 1974. Australian specimens deposited at NHM, London.

Diagnosis. Ventral surface of cephalosome with wrinkles parallel to edge, hyaline border with striations parallel to edge; lateral striations on female genital double-somite 10% of animal's length; Hicks index for α on female caudal ramus = 52%; α and β setae on male caudal ramus short (⅓ length of ramus); δ seta on segment 3 of male antennule about same length as segment 2; setules absent from anterior lobe of mandible; antenna endopod segment 2 without extensive area of setules; no row of setules on lateral surface of maxilliped basis.

Biometric data. Data for Australian specimens, (values for Japanese specimens within square brackets).

Females (N = 29 [27]): maximum length (L_{max}) mean 0.59 mm [0.61 mm], body length (L_{urs}) mean 0.57 mm [0.58], range 0.53–0.58 mm; cephalosome width (W) mean 0.35 mm [0.39 mm]; rostrum width (R) 0.060 mm [0.065 mm]; genital double-somite width 0.22 mm; caudal ramus length 0.16 mm, width (max) 0.065 mm.

Ratios: (L_{max})/W 1.65, (L_{urs})/W 1.52; caudal ramus l/w 2.4 [2.2], Hicks index for α 52% [52%]; number of eggs carried by female 6 [6].

Males (N = 14 [16]): maximum length (L_{max}) mean 0.44 mm [0.42 mm], range 0.40–0.47 mm, body length (L_{urs})

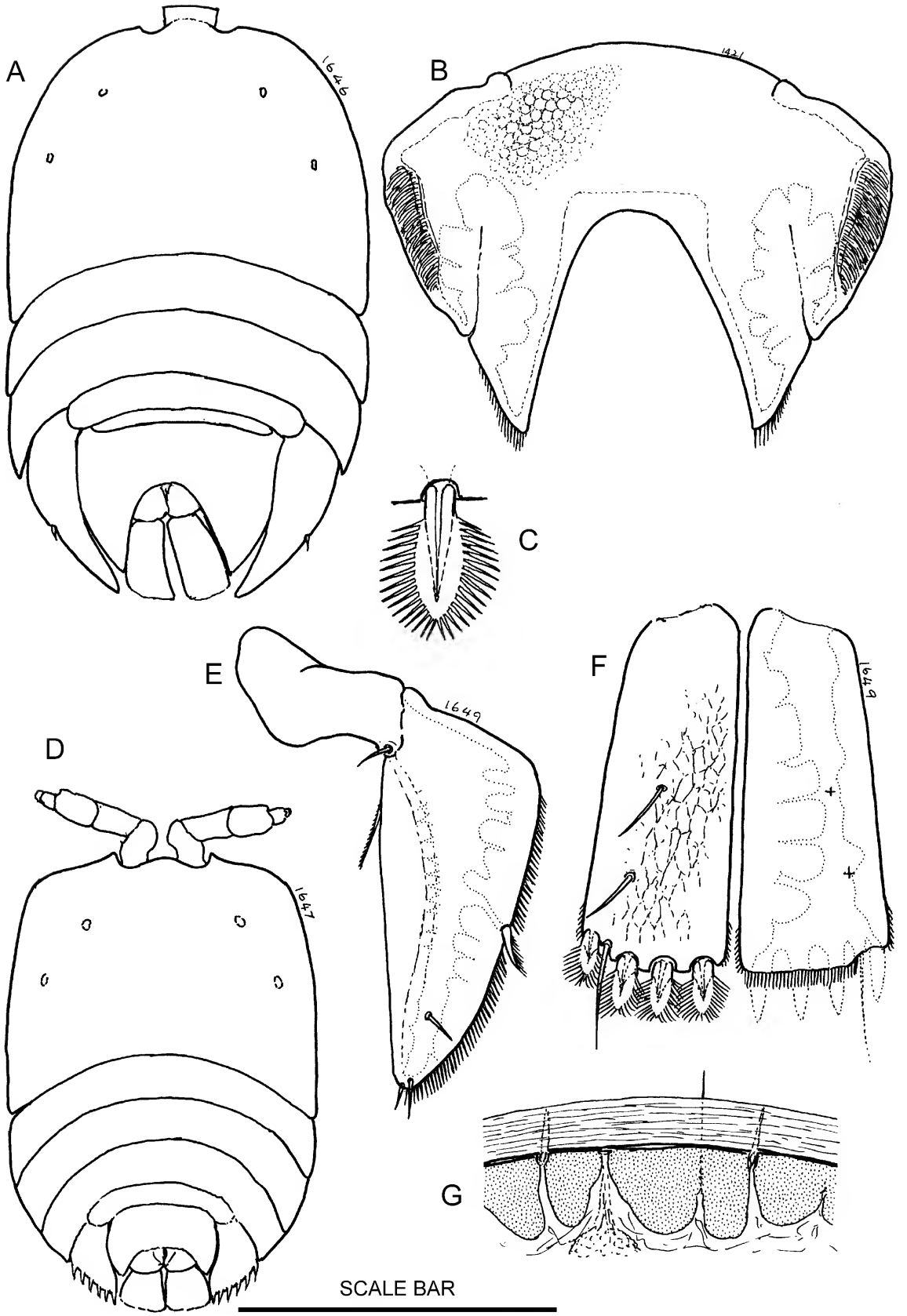

Figure 30. *Clavigofera pacifica* Harris & Iwasaki, 1996, (Australian specimens). Female: *(A)* adult; *(B)* genital double-somite; *(C)* pinnate clavate seta from caudal ramus; *(E)* P5 (dorsal); *(F)* caudal rami (dorsal left, ventral right); *(G)* hyaline border with parallel striations. Male: *(D)* adult. Scale bar: A, D = 0.32 mm, B = 0.18 mm. E = 0.15 mm, F = 0.14 mm, G = 0.06 mm. (*C* not to scale).

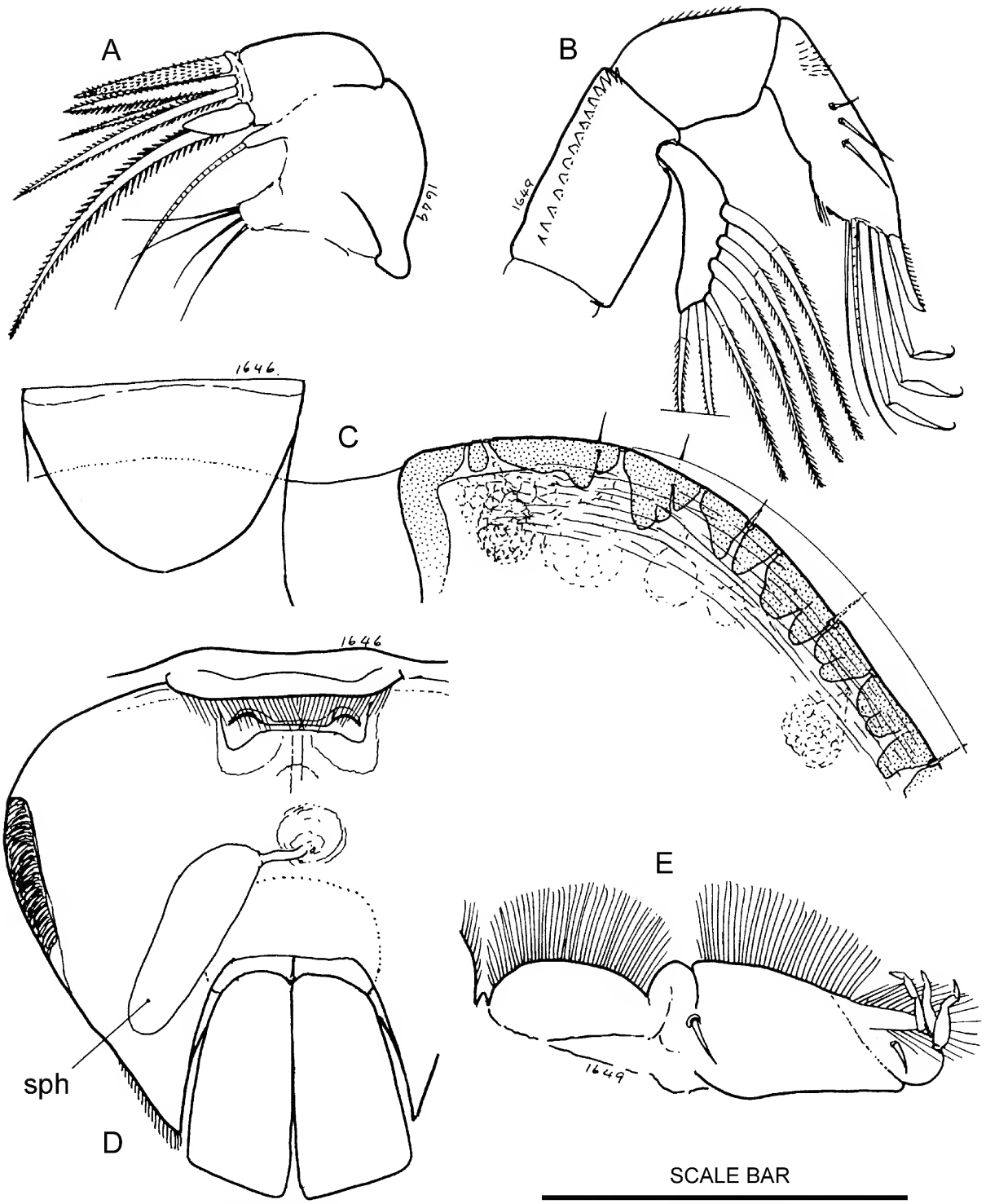

Figure 31. *Clavigofera pacifica* Harris & Iwasaki, 1996. Female: *(A)* maxilla; *(B)* antenna; *(C)* rostrum and "shoulder" (ventral); *(D)* genital double-somite with spermatophore attached (ventral view); *(E)* maxilliped. Scale bar: A, B, E = 0.07 mm. C = 0.04. D = 0.18 mm.

mean 0.39 mm [0.38 mm]; cephalosome width (W) mean 0.32 mm [0.31 mm]; antennule length (N = 6) 0.123 mm; spermatophore length 0.08 mm.

Ratios: (L_{urs})/W 1.22; antennule 28% of (L_{urs}) [measurements of male antennule segments made on two paratype specimen from Japan fall within the range of animals from Australia], segment 2 37%, segment 3+4 36%, dactylus 17%, aesthetasc 68% of antennule length, δ seta = length of segment 2, spermatophore 21% of (L_{urs}).

Description. *Adult females* (Fig. 30A): colour pale yellow or colourless. Anterior of cephalosome slightly truncated, rostrum very narrow (18% of cephalosome width). Sides of body outline almost parallel. Hyaline border with striations parallel to edge (Fig. 30G), 10 µm wide, dorsal pits conspicuous, 5–6 µm. Ventral surface of cephalosome

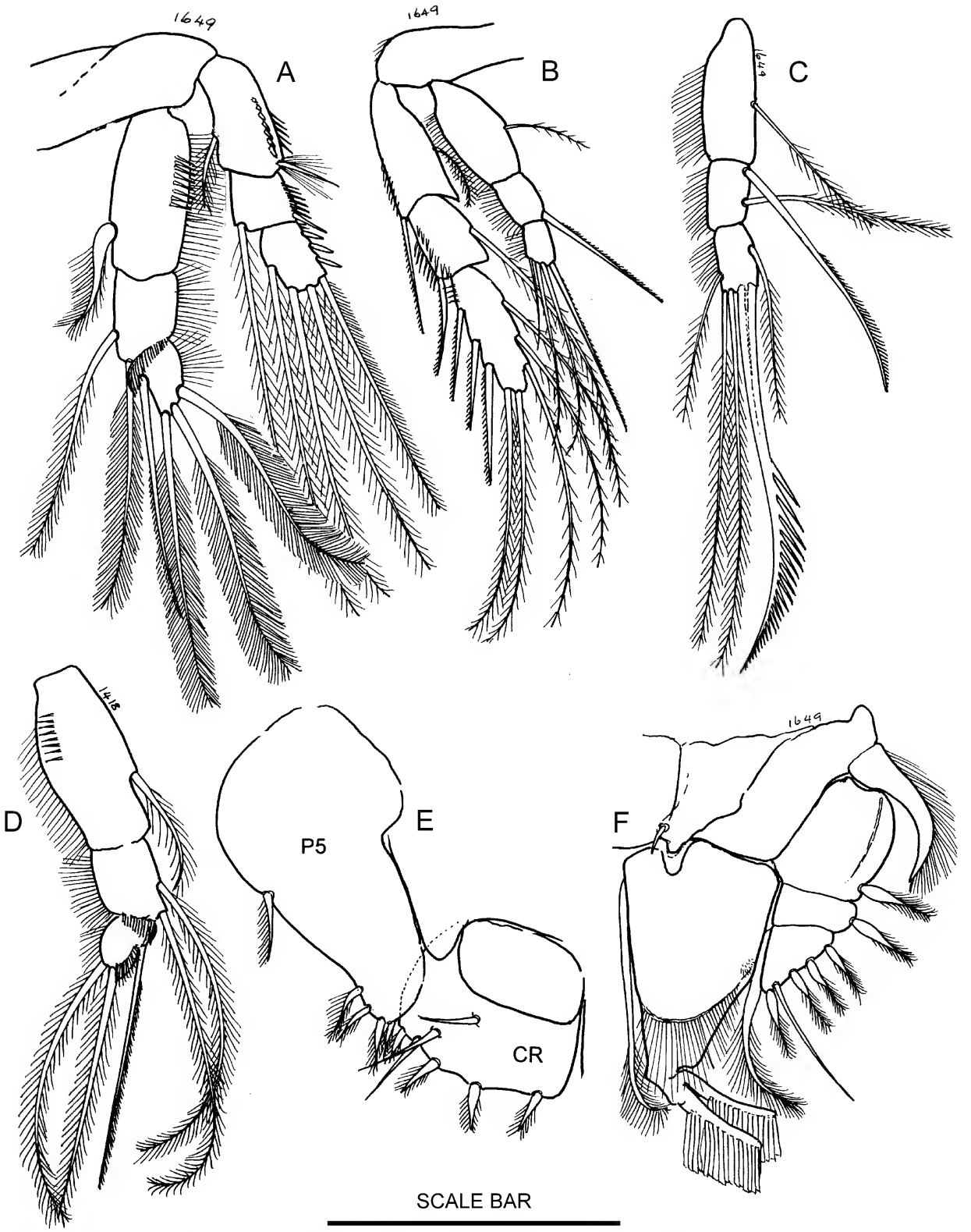

Figure 32. *Clavigofera pacifica* Harris & Iwasaki, 1996. Female: *(A)* P2; *(B)* P4; *(C)* P3 endopod; *(E)* P5 and caudal ramus of stage V female copepodid; *(F)* P1. Male: *(D)* P2 endopod. Scale bar: A, D = 0.1 mm. B, C, E = 0.08 mm. F = 0.09 mm.

with wrinkled cuticle parallel to border (Fig. 31C). Lateral band of striations (striated rugose band) on ventral surface of genital double-somite anterior lobe 33% of somite length, dorsal surface of genital double-somite pitted. Notch and broad scar indicate boundary between anterior and posterior lobes (Fig. 30B), posterior lobe narrow, straight sided, acutely pointed posteriorly, bordered with fine setules. Posterior arch deep, encloses almost ¾ of caudal furca. Sternal sclerite of metasome segment 4 fimbriate on posterior edge (Fig. 31D). Caudal rami rectangular, widen posteriorly (Fig. 30F),

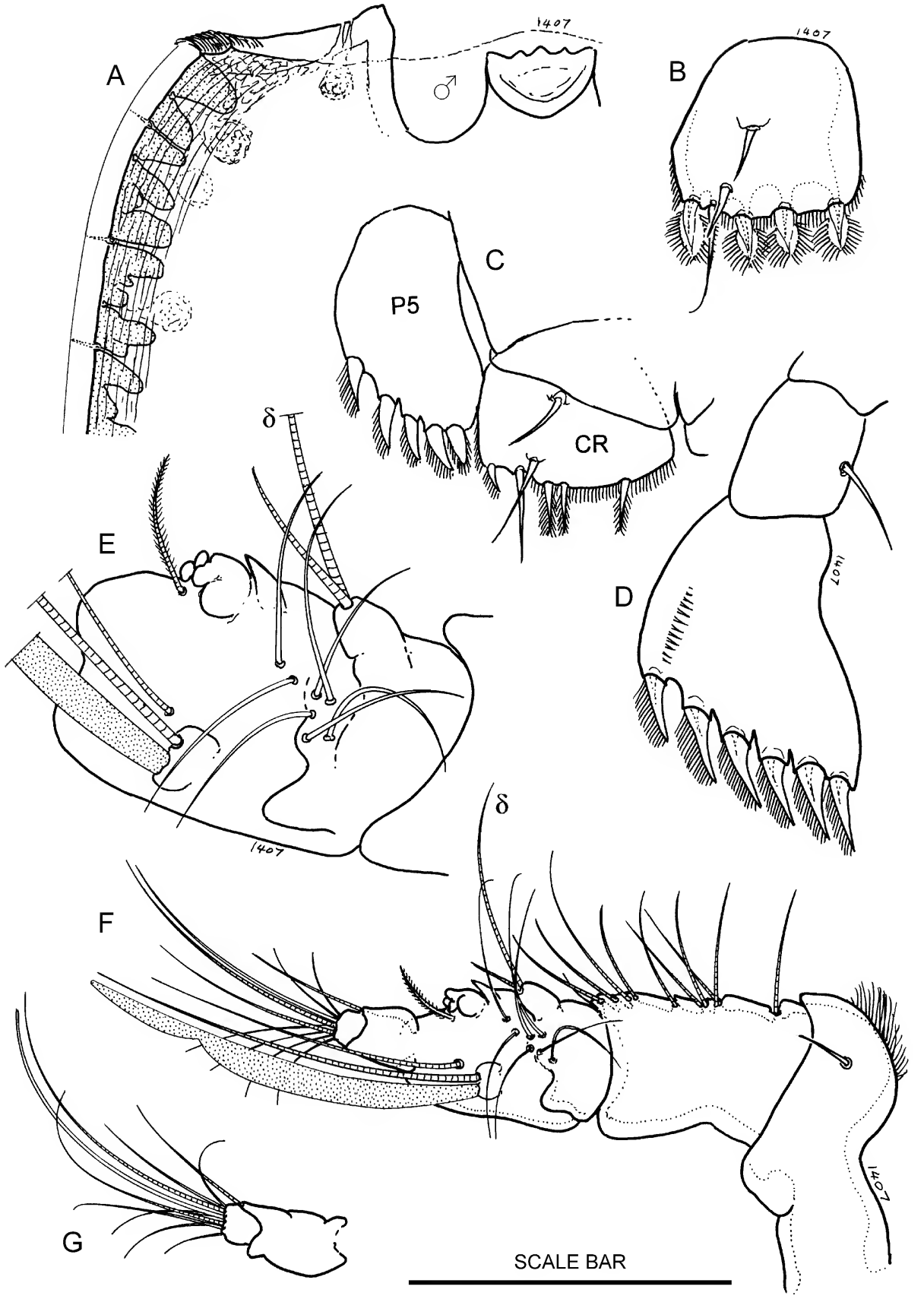

Figure 33. *Clavigofera pacifica* Harris & Iwasaki, 1996. Male: *(A)* rostrum and "shoulder" (ventral); *(B)* left caudal ramus; *(C)* P5 and caudal ramus of stage V male copepodid; *(D)* P5; *(E, F, G)* antennule (*E*, detail of segment 4; *G*, dactylus). Scale bar: A, C, D = 0.07 mm. B, F, G = 0.08 mm. E = 0.04 mm.

posterior border slightly convex with terminal fringe of setules. Terminal setae T1–T4 large, pinnately clavate (Fig. 30C), evenly spaced along posterior edge [terminal setae of copepodids are not pinnate clavate], α seta about half way down ramus. Structure and setation of mouthparts and ambulatory limbs typical of family. Segment 2 of antenna endopod with a few surface setules, no extensive rows of setules (Fig. 31B). Mandibular palp without setules on anterior lobe. Maxillule with single bulbous seta on exopod. Seta on distal endite of maxilla plain, not comb-like (Fig. 31A). Maxilliped without lateral row of surface setules on basis (Fig. 31E). Very small patch of denticles at lateral end of fimbriate crescent on P1 endopod (Fig. 32F). Serrulate spinous terminal seta on P2 endopod ¾ length of endopod (Fig. 31A). Serrulate spinous seta on segment 2 of P3 endopod shorter than endopod (0.85:1), large serrate spinous seta on segment 3 of endopod much longer than endopod (1.5:1) (Fig. 32C). Seta on segment 2 of P4 endopod and first internal seta on segment 3 finely serrulate, spinous (Fig. 32B). Exopod of P5 lanceolate, dorsal surface pitted, one dorsal seta plus subapical and smaller apical seta (Fig. 30E), apex of P5s reach beyond posterior extremity of genital double-somite but do not touch one another. Females carry six eggs.

Adult males (Fig. 30D). Colour, hyaline border, dorsal pits and wrinkled ventral edge of cephalosome as described for female. Cephalosome truncated, anterior edge turned ventrally, lateral angle of antennule socket prominent, shoulders sharply rounded (Fig. 33A). Caudal rami quadrate (l/w = 1) with lateral edge convex, dorsal surface pitted, α and β setae short (less than half length of ramus), terminal setae T1–T4 pinnately clavate, equal in size and equally spaced (Fig. 33B). Limbs as for female except for the following. Antennule held in characteristic posture when not folded ventrally (Figs 30D, 33F), segment 2 as long as segment 4 + dactylus, segment 3 with very short ventral process, δ seta short (= length of segment 2), aesthetasc nearly twice length of segment 2, coupling denticles on segment 4 very small, proximal pointed, distal rounded, dactylus short with segments 5 and 6 distinct (½ length of segment 2) (Figs 33E, F, G). Endopod of P2 with two plumose and one serrulate spinous seta on segment 3 (Fig. 32D). Spermatophore about ⅕ length of animal.

Remarks. Detailed descriptions of *Clavigofera clavigera, C. laurencia* and *C. ulva* that would confirm their validity were not given. A full description of these species is needed to justify use of Hicks' index to separate them.

Stage IV and V male and female copepodides have slender pinnate terminal setae on their caudal rami (Figs 32E, 33C). The characteristic pinnately clavate terminal setae of adults appear at metamorphosis.

Distribution. *Clavigofera pacifica* is widely distributed on the coasts of Japan. Australian specimens have been collected from the mid and northern coast of NSW.

The species has been recorded as abundant on *Lobophora variegata* at the following localities: Broulee rock platform (35°52'S 150°71'E) 47 ♀♀, 22 ♂♂, 6 coupled ♂♂; Shelly Beach, Cronulla, Sydney (34°03'S 151°11'E) 103 ♀♀, 85 ♂♂, 41 coupled ♂♂; Arrawarra Headland (30°03'S 155°02'E) 122 ♀♀, 70 ♂♂, 74 coupled ♂♂, V. A. Harris 1974, 1976, 1982. The species has been collected from a number of other seaweeds in smaller numbers. On *Caulerpa* sp., at Broulee, and Ballina (28°52'S, 153°36'E) also on *Gelidium* sp., at Nambucca Heads (30°39'S 153°01'E) V. A. Harris 1982.

Discussion

Three of the new species described here are of particular interest because they belong to genera already known from Japan and Korea. They are clearly defined by apomorphic character states that exclude them from other genera including *Porcellidium* (see Harris, 2014).

The genus *Kushia*, characterized by an anterior comb on segment 3 of male antennule, has three species in Japan. It is represented in NSW, Australia by *Kushia spathoides* sp. nov. A second genus, *Kensakia*, characterized by a unique brush-pad on segment 4 of the male antennule, has two species in Japan and Korea, and one each from Sri Lanka and Malaysia. It is represented in Queensland by *Kensakia australis* sp. nov. A new genus, *Synurus* has been erected to accommodate the third species, *Synurus ctenocheirus* sp. nov., which shows two features that are considered autapomorphic (i.e., fusion of male P5 baseoendopod with metasome segment 4 and genital somite, and atrophy or loss of five terminal setae from the male P5 limb). This species was collected from the Great Barrier Reef at Cairns, Queensland, but it has also been found on Okinawa Island, Japan (specimens in Yuka Sasaki's personal collection examined by author. Sasaki confirms that measurements of her animals fall within the range given in text above). The only other species known to occur in both Japanese and Australian waters is *Clavigofera pacifica* Harris & Iwasaki, 1996 and reported here from NSW for the first time.

The male antennule in porcellidiid taxonomy. In the study of Australian and Japanese species it was found that the female antennule is remarkably uniform in its structure and setation throughout the family and is of little taxonomic importance. On the other hand, the highly modified antennule of adult male animals shows an extremely wide range of structure that provides more useful taxonomic characters than any other part of the body. Of 60 species for which the detailed structure of the male antennule is known, segment shape, type and number of setae, shape and position of chitinous tooth-like structures (coupling denticles), was found to be specific for each species. Consequently, the identity of any male animal can be determined with certainty if the male antennule of the species has been described. In contrast, not all female animals can be identified with certainty from female characters alone. A detailed description of the male animal becomes an absolute requirement for a valid description of any porcellidiid.

In the Porcellidiidae the antennule of both male and female animals is reduced to six morphological segments, but the partial fusion of segments 3 and 4 and (in most species) segments 5 and 6 of male animals gives the impression that there are only four or five segments (Fig. 29E). Segment 3 cannot be seen from dorsal view, but in ventral view it appears as a separate structure bearing the δ and δ' setae on an anterior process plus a group of five to seven π setae, and (in some species) a single coupling denticle. Hicks & Webber (1983) describe this segmant as a "lappet" of segment 2, but its setation shows it to be segment 3. In the majority of species segments 5 and 6 are fused (referred to as the dactylus), but in others species segment 6 is distinct (Fig. 33G).

The male antennule is subchirocer with the neocopepodan articulation between segments 4 and 5, Huys & Boxshall (1991). It is prehensile with segment 4 greatly enlarged

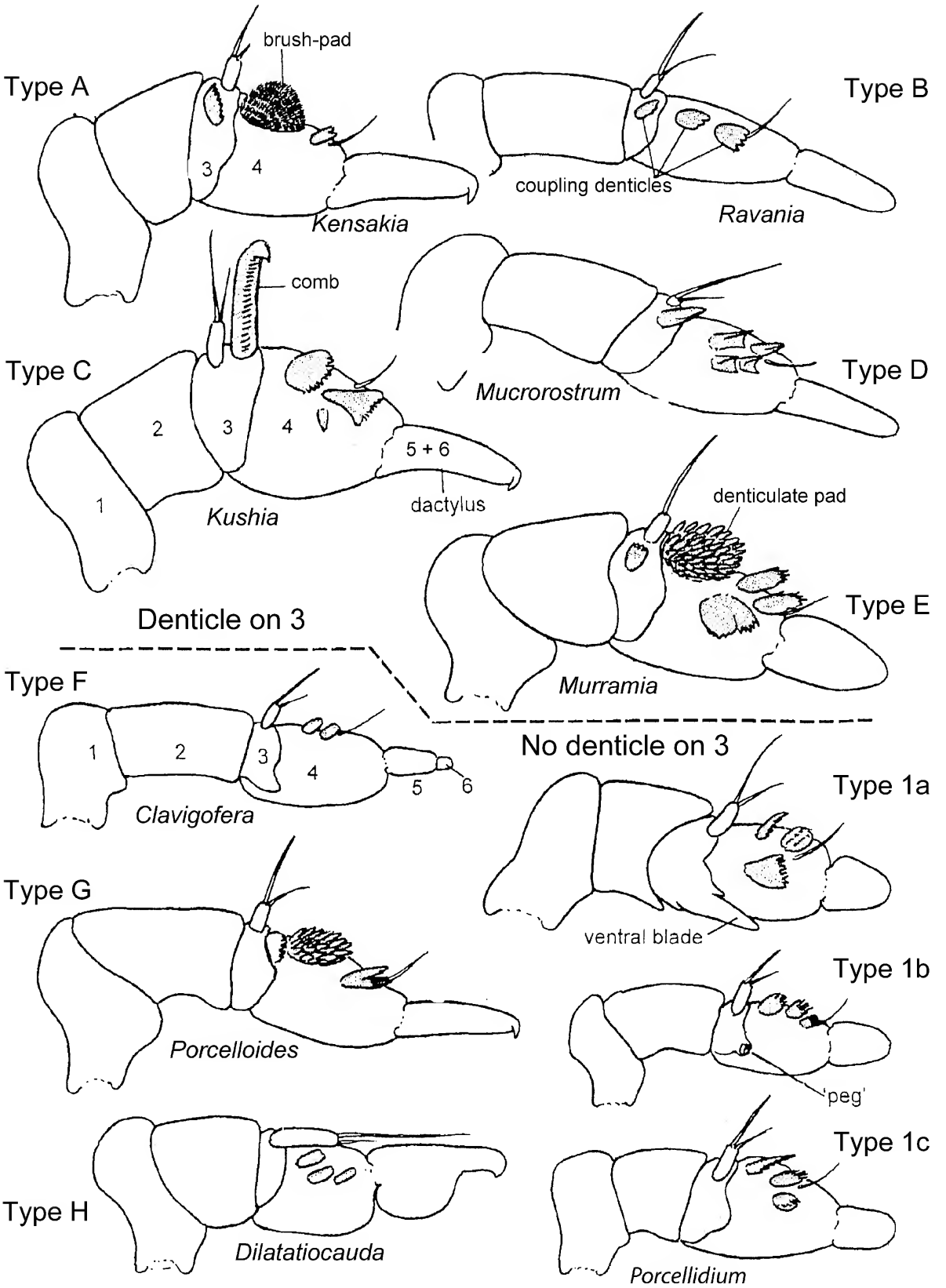

Figure 34. Characteristic arrangement of male coupling denticles in certain genera (diagrammatic, see text). Type A, *Kensakia*; Type B, *Ravania*; Type C, *Kushia*; Type D, *Mucrorostrum*; Type E, *Murramia*; Type F, *Clavigofera*; Type G, *Porcelloides*; Type H, *Dilatatiocauda*; Types 1a, 1b, 1c, *Porcellidium*.

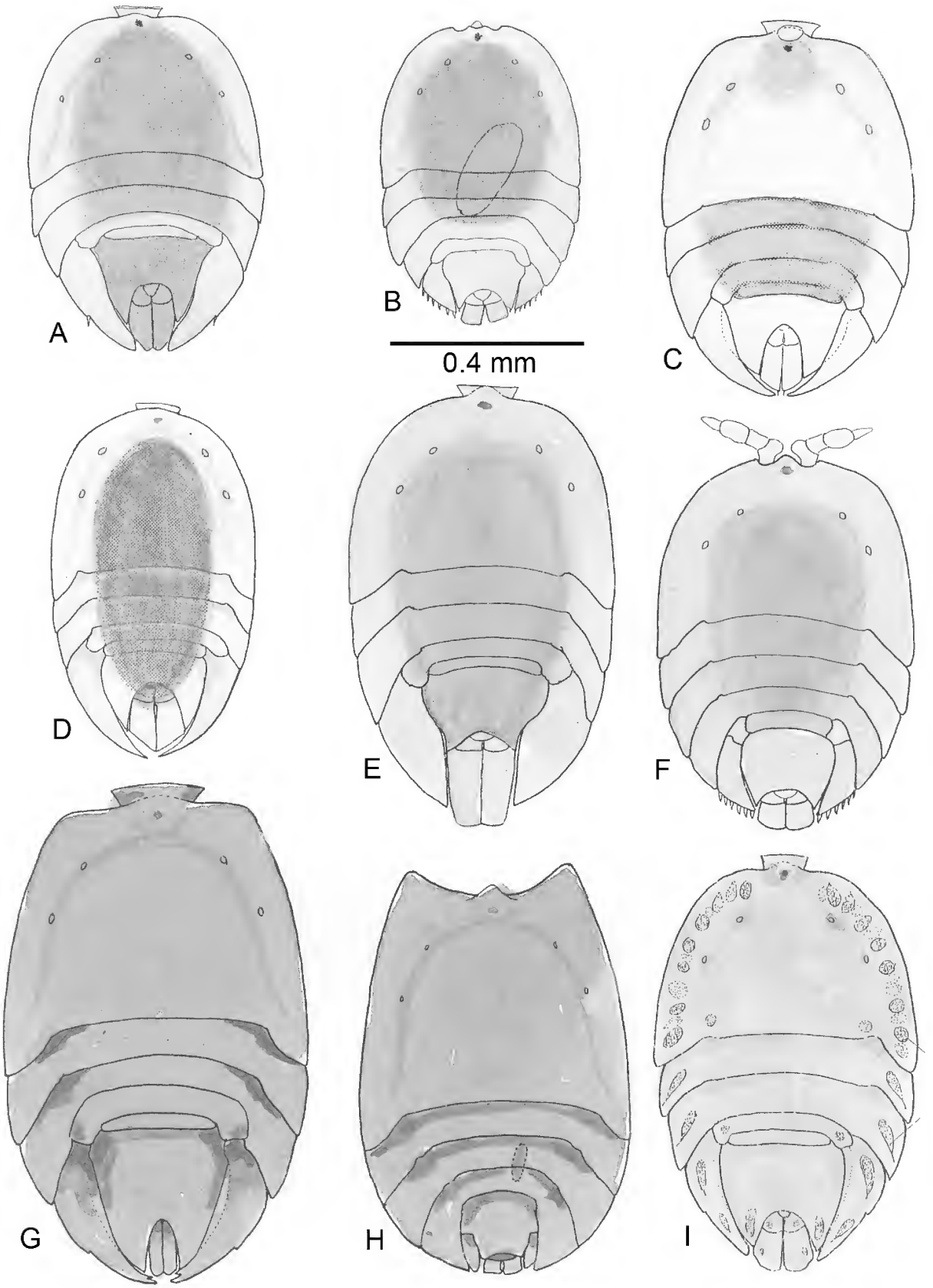

Plate 1. *(A) Ravania wellsi* sp. nov., female; *(B)* male. *(C) Acutiramus bipunctatus* sp. nov., female. *(D) Kensakia australis* sp. nov., female. *(E) Ravania doliocauda* sp. nov., female; *(F)* male. *(G) Synurus ctenocheirus* sp. nov., female; *(H)* male. *(I) Kushia spathoides* sp. nov., female. *A–I* Australian species. Scale bar: 0.4 mm.

to accommodate the massive adductor muscle that closes the finger-like dactylus against the ventral side of segment 4. This enables the male to grip the posterior region of a juvenile female during mate guarding behaviour. The number and position of setae on the antennule is more or less constant throughout the family, but setae may differ from species to species in type (plain, annulate, plumulose) and length (compare Figs 28G and 29B). The chitinous coupling denticles are not modified setae, they appear *de novo* at the final moult or metamorphosis of the male from stage V copepodid to adult, Harris (1994). They are only found on the ventral side of segments 3 and 4. Many species do not have a denticle on segment 3, but when it is present, there is never more than one. Segment 4, however, always has one to five denticles. The shape of these denticles varies widely, from simple thorn-like structures to complex brush-like pads, clusters of denticles (denticulate pads), flat plates with plain or serrated edge, comb-like denticles, plain tooth-like denticles and even small balloon-like structures (Fig. 12G).

It is assumed the coupling denticles enable the male to grip the female copepodid more effectively by increasing friction. There is no evidence for a "locking mechanism" as there is no corresponding depressions on the juvenile's P5 or posterior region of the body into which the denticles could fit. Apart from differences in size and shape between juvenile stages, there is surprisingly little variation in shape or structure of the abdominal region between species of female copepodids. This suggests the variability of the male's coupling denticles is not connected with a species isolating mechanism or a mechanism whereby adult males can distinguish between male and female copepodids.

When the male antennule is compared between species, a clear correlation can be seen between certain arrangements of denticles (number and shape) and particular genera. The clearest example of this is seen in the genus *Kushia* with four described species. The genus is defined by the unique ventral expansion on the female P5 (Fig. 16E), but the characteristic anterior comb on segment 3 of the male antennule is equally unique (Fig. 18E, F); both can be regarded as apomorphic characters. Similarly, the brush-pad only found on segment 4 of all species of *Kensakia* should be considered autapomorphic. A remarkable similarity in the arrangement of denticles can be seen in species belonging to other genera. In Fig. 34 the typical arrangement of denticles is shown diagrammatically for certain porcellidiid genera. The arrangement of denticles can be divided into two groups: those with one denticle (or comb) on segment 3 and those without a denticle on segment 3. In each group segment 4 may have two, three, four or five denticles. In the first group *Kensakia* (type A) and *Ravania* (type B) have only two denticles. *Kushia* (type C) has three denticles of characteristic shape. *Mucrorostrum* (type D) and *Murramia* (type E) both have four denticles, but the shape of the denticles is very different in the two genera (*Murramia* is unique in lacking the δ' seta). The second group, without a denticle on segment 3, is less clearly defined but *Clavigofera* (type F) appears to have two denticles on segment 4 (the antennule has not been described for all the known species). *Porcelloides* has three characteristically shaped denticles (type G). *Porcellidium* (type Ia, Ib, Ic) also has three denticles but their shape is much more variable. This genus may have a ventral process to segment 3 in the shape of a "blade" or "peg", but this is not unique to *Porcellidium* for it is found in *Tectacingulum*, *Acutiramus*, *Synurus* and *Dilatatiocauda*. The latter genus shows another unusual feature, the anterior process carrying δ and δ' setae lies parallel to the axis of the antennule (horizontal); in most other species the process and δ seta project forwards.

Because the configuration of the setae and denticles is unique for each species, male animals have been chosen as the holotype for each of the new species described above.

Acknowledgment. I am grateful to Yuka (Tadasugi) Sasaki for allowing me to examine her extensive collection of Porcellidiidae from Japan.

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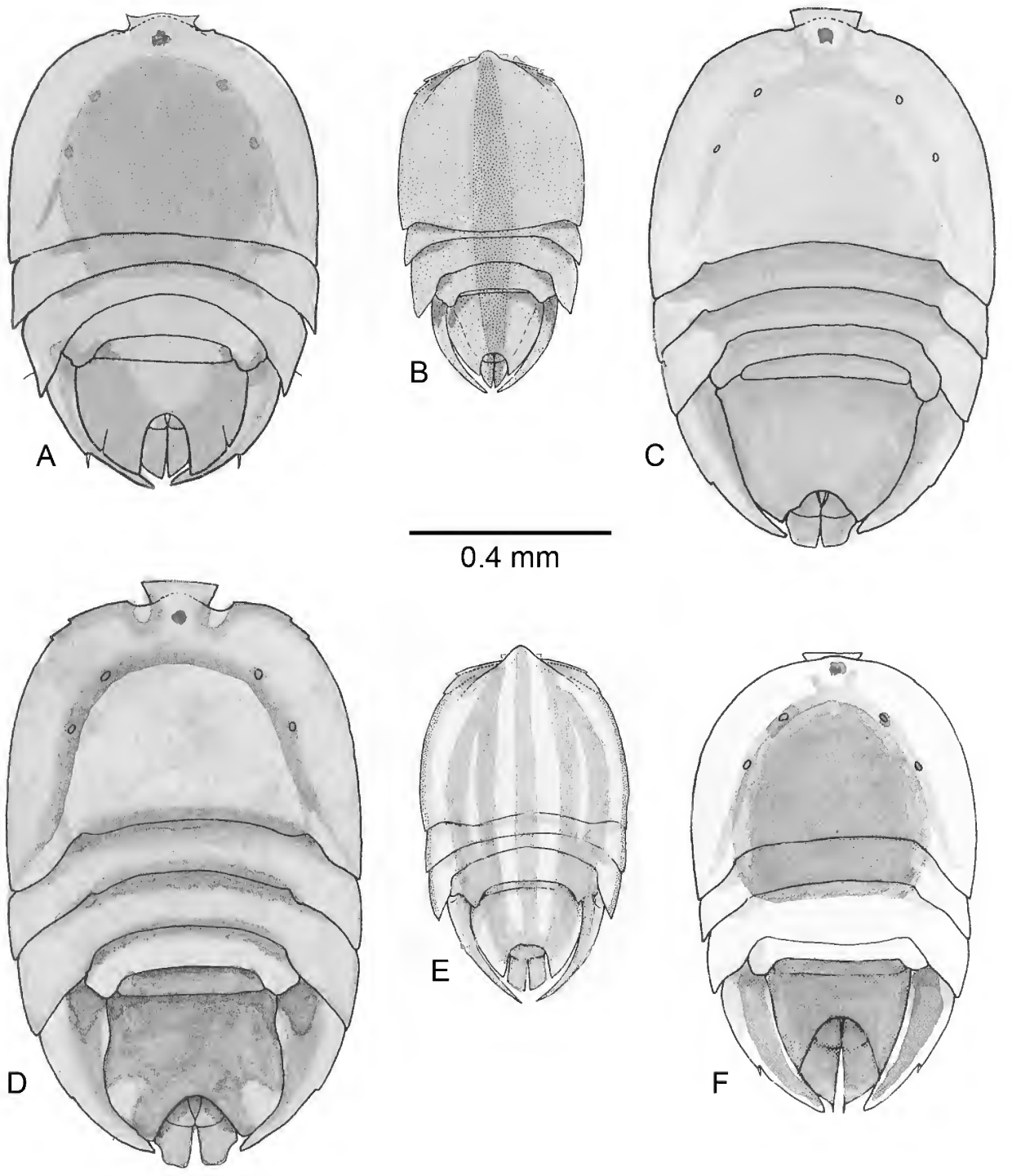

Plate 2. *(A) Acutiramus sesquimaculatus* (Harris, 1994), female, Australia. *(B) Acutiramus rufolineatus* Harris & Robertson, 1994, female, Australia. *(C) Kushia igaguria* Harris & Iwasaki, 1996, female, Japan. *(D) Kushia zosteraphila* Harris & Iwasaki, 1996, female, Japan. *(E) Acutiramus quinquelineatus* Harris & Robertson, 1994, female, Australia. *(F) Kensakia acuta* (Kim & Kim, 1997), female, Korea and Japan. Scale bar: 0.4 mm.

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Porcellidiidae of Australia (Harpacticoida, Copepoda). III. Synopsis of Genera and Species

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Abstract. Three new species belonging to the Porcellidiidae are described. A species from NSW possessing massive honeycomb-like dorsal growths of cuticle, and other features not found elsewhere in the family, has been placed in a new genus, *Cereudorsum verrucosum* gen. *et* sp. nov. A second species from Queensland, characterized by unusual features of the male antennule, has been placed in a new genus, as *Geddesia quadrata* gen. *et* sp. nov. *Porcellidium trisetosum* Geddes, 1968 does not fit the diagnosis for *Porcellidium* and is transferred to *Geddesia* gen. nov., as *G. trisetosa* (Geddes, 1968) comb. nov. A third species from the Cocos Keeling Islands is unique in having only one seta on the maxillule endopod. It has been referred to a new genus, as *Clunia cocosensis* gen. et sp. nov. This brings the total number of genera described from eastern coast of Australia to 16.

A key to the genera, a list of the apomorphic or unique characters of each genus and a check list of the identifiable species of Porcellidiidae is given. The geographical distribution of species along the east coast of Australia is outlined.

Keywords: Porcellidiidae, *Cereudorsum, Clunia, Geddesia, Porcellidium.*

Harris, Vernon A. 2014. Porcellidiidae of Australia (Harpacticoida, Copepoda). III. Synopsis of genera and species. *Records of the Australian Museum* 66(2): 167–196.

It is now recognized that the family Porcellidiidae has more than one genus, although there is some disagreement as to their number. Bodin (1997) lists eight but Wells (2007) only recognizes six and considers *Acutiramus, Kensakia, Kioloaria, Murramia* and *Mucrorostrum* synonyms for *Porcellidium* on the grounds that they were not defined according to the Hennigian system. The real problem, however, was the lack of agreement between authors over the concept of *Porcellidium*. Our knowledge of these characters is based on Brady's (1880) incomplete and inaccurate description of his *Porcellidium viride*. However, Brady does show one unique species specific feature on the male antennule that allows the species to be identified with certainty. This fact has been used to redescribe the male *Porcellidium viride* in detail and give a definitive diagnosis for the genus (Harris, 2014a). The new diagnosis highlights the fact that more than half of the species formerly placed in *Porcellidium* no longer belong to that genus and must be moved elsewhere. The five genera listed above each possess apomorphic characters, not found on the type species *P. viride*, which exclude them from the genus *Porcellidium*. By 2002 ten genera had been described and prior to this paper another three had been added (Harris, 2014a,b). The three new species described here present a similar problem: they possess characters considered apomorphic which exclude them from all previously described genera.

Based on over 60 species for which reliable data on the male antennule are now available, a reassessment of all the proposed genera can be made to determine their validity. Walker-Smith (2001) pointed out that the genera proposed by Harris & Robertson (1994), Harris (1994) and Harris & Iwasaki (1996) were defined on a collection of characters

and not autapomorphies. To overcome this problem, type material has been re-examined for each genus to assess whether the diagnostic characters chosen can be considered autapomorphic or not. This is relatively simple for genera with several species that possess the same character set as the type species, but not for genera based on a single species. The three new species described here will illustrate this problem. They do not fit the diagnosis of any existing genus, but display unique features that suggest each should be placed in a separate genus.

A revised list of the apomorphic and autapomorphic characters for each of the genera is given to bring their definition into line with Hennigian principles (Table 1). This enables the 71 species of Porcellidiidae recognized in this study to be placed in the appropriate genus. The genus to which a species excluded from Porcellidium has been placed is shown in a check list (Table 2).

The family is well represented on the eastern coast of Australia where 32 species have been described. Their distribution along the coast is discussed.

Methods and terminology

Methods and terminology follow Harris & Robertson (1994) and Harris (2014a,b). Measurements of caudal ramus and genital double-somite are taken from dissections, laid flat and the male antennule fully extended. The following method was used to extend the antennule. Seaweed was washed in a 50/50 mixture of soda water saturated with CO_2 (from soda siphon or bottled soda water) and fresh water. This appears to anaesthetize the copepods which were then fixed in 5% formalin with their antennules fully extended. Drawings and measurements were made from calibrated digital photographs of paratype specimens mounted in 50% glycerol or dissections mounted in polyvinyl lactophenol. Two measurements of length are given, L_{max} from rostrum to posterior extremity of caudal furca and L_{urs} from rostrum to posterior extremity of the genital double-somite. Scanning electron micrographs (Plates 1 and 2, pp. 172–173) were taken on an Hitachi S225 ON SEM from gold coated, formaldehyde fixed material. The abbreviation AM for Australian Museum, Sydney and NHM for the Natural History Museum, London are used.

No information is available for the manner in which the three specimens from Cocos Keeling Islands were obtained or their exact location.

Systematics

Family Porcellidiidae Boeck, 1865

Genus *Cereudorsum* gen. nov.

Type species. *Cereudorsum verrucosum* sp. nov.

Diagnosis. Dorsal organs present (trough-like depressions in cuticle), surrounded by massive honeycomb-like cuticle (Figs 1A, 4F); male antennule unique, no denticle on segment 3, segment 4 with group of four or five swollen finger-like structures in place of typical cuticular denticles; maxilliped coxal lobes wide apart; no ridge plates on labrum; male and female caudal ramus rectangular, T1 small pinnate, deeply recessed, setae T2, T3 and T4 large pinnate, equally spaced (not pinnately clavate); maxillule with six setae on endopod; male P5 trapezoid, no reduction in number of terminal setae; spermatophore elongate, ephemeral on female.

Species composition. Only the type species is known, *Cereudorsum verrucosum* sp. nov. Recorded from Sydney, NSW, Australia.

Etymology. *Cereudorsum*, (L. *cereus* = waxen, honeycomb + *dorsum* = the back).

Remarks. Dorsal organs surrounded by massive honeycomb-like growth of cuticle are not known elsewhere in the Porcellidiidae; their presence is considered an autapomorphic character that defines the genus.

Superficially, the large pinnate terminal setae (T2–T4) on the caudal rami resemble the pinnately clavate setae of *Clavigofera* but in the latter genus the pinnae arise from a flattened expansion of the seta shaft, not the shaft itself (Fig. 12R), and T1 is the same size and shape as T2–T4.

The maxillipeds of *Cereudorsum* resemble those of *Dilatatiocauda*, which do not meet in the midline or possess a fimbriate process, but the basis is elongated typical of other Porcellidiidae.

Cereudorsum verrucosum sp. nov.

Figs 1–5; Plates 1, 2

Type material. HOLOTYPE adult male, length 0.73 mm, P81216; ALLOTYPE adult female, length 0.92 mm, P81217; PARATYPE specimens 10 ♀♀, 6 ♂♂, P81218, deposited at AM, Sydney. Additional paratypes deposited at NHM, London. All collected from rotting *Ecklonia radiata* near entrance to Gunnamatta Bay, Port Hacking, Sydney, New South Wales (34°05'S 151°08'E), V. A. Harris, 1977.

Diagnosis. Female with blocks of microtubules near edge on anterior half of cephalosome, microtubules absent from male cephalosome; both male and female have two dorsal organs with honeycomb-like cuticle on cephalosome and one each on metasome segment 3 and genital double-somite; numerous dorsal sensilla (> 100) on cephalosome, metasome and genital double-somite; female caudal rami with two longitudinal ridges; internal seta absent from segment 1 of male and female P4 endopod; first (lateral) seta on male P5 with five strong ventral setules, each terminal seta with row of three setules at its base.

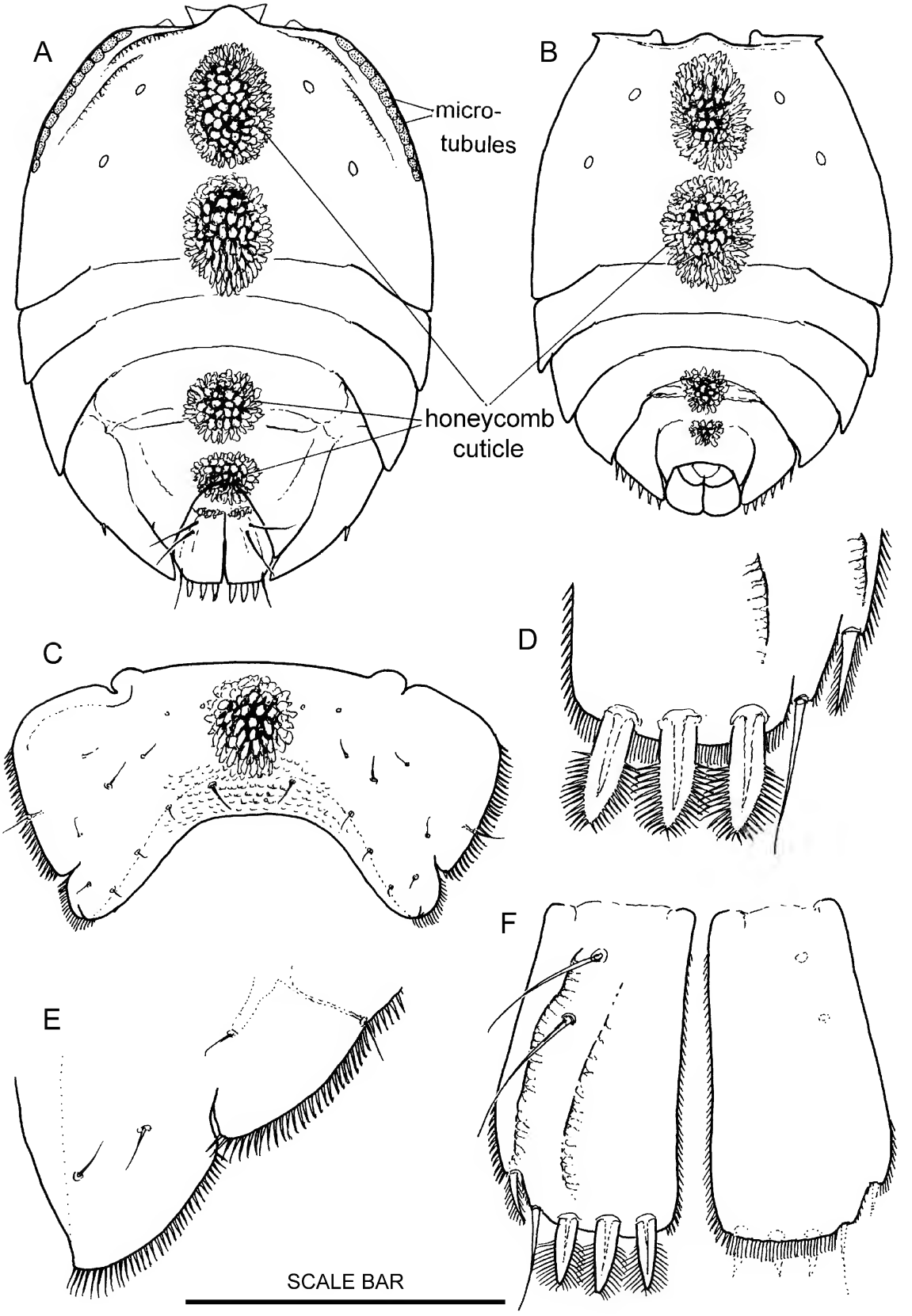

Figure 1. *Cereudorsum verrucosum* sp. nov. Female: *(A)* adult; *(C, E)* genital double-somite (*E* detail of posterior lobe); *(D, F)* caudal rami (*D* detail of terminal setae). Male: *(B)* adult. Scale bar: A, B = 0.5 mm. C = 0.03 mm. D = 0.08 mm. F = 0.14 mm.

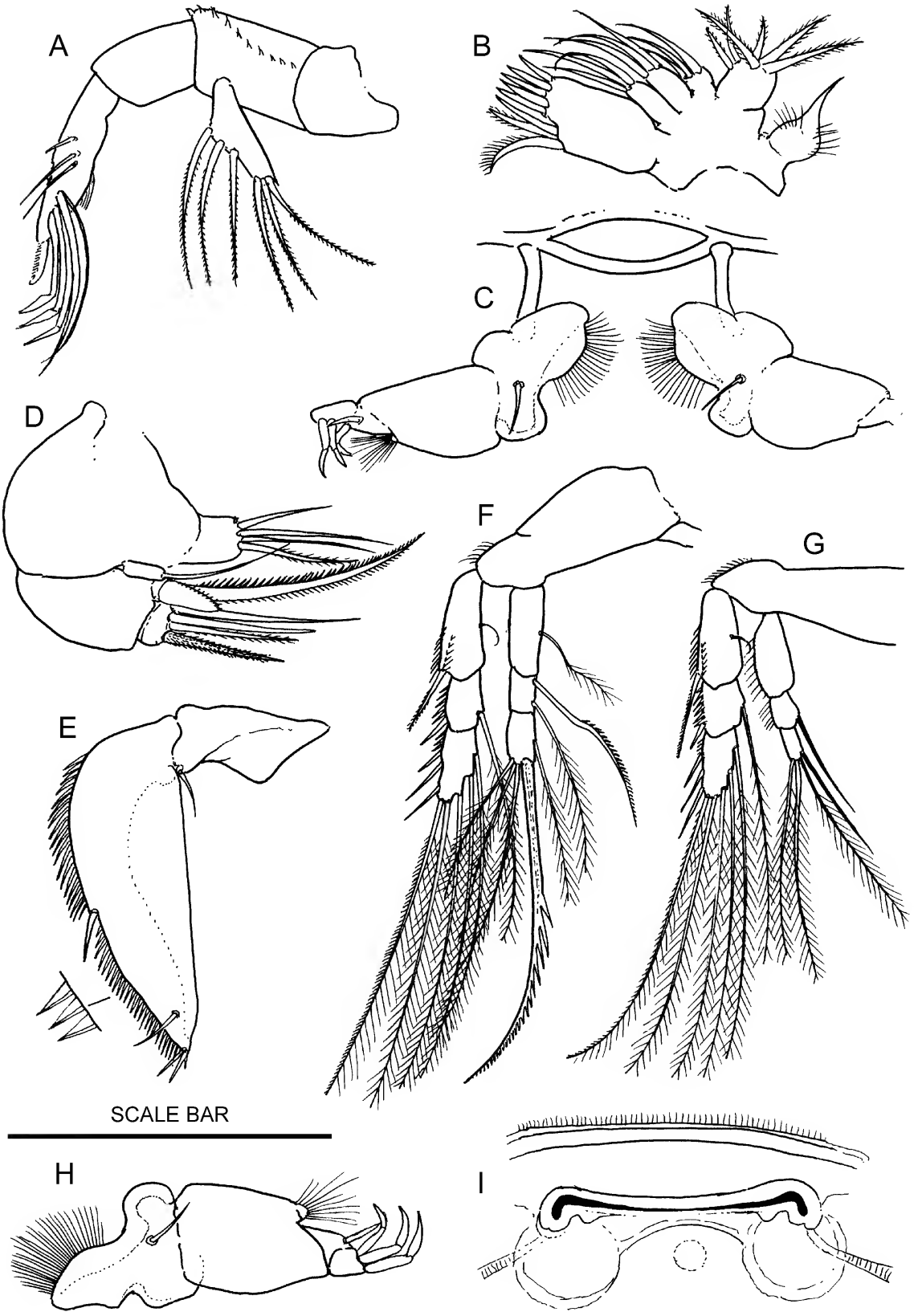

Figure 2. *Cereudorsum verrucosum* sp. nov. Female: *(A)* antenna; *(B)* maxillule; *(C)* maxillipeds (note, coxae do not touch); *(D)* maxilla; *(E)* P5 and detail of border setules; *(F)* P3; *(G)* P4; *(H)* maxilliped; *(I)* genital opening. Scale bar: A, C = 0.14 mm. B = 0.08 mm. D, H, I = 0.1 mm. E = 0.3 mm. F, G = 0.23 mm.

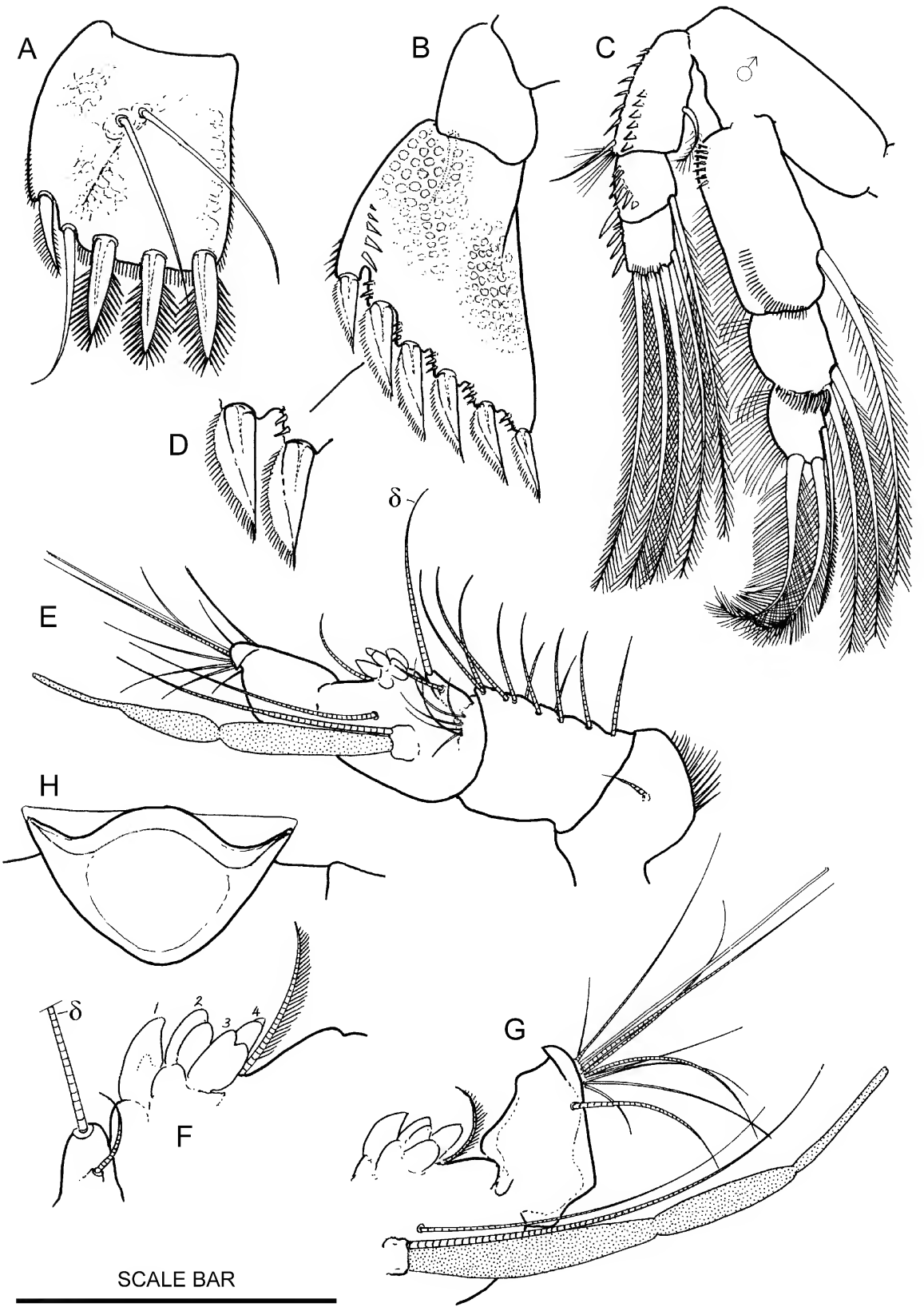

Figure 3. *Cereudorsum verrucosum* sp. nov. Male: *(A)* caudal ramus; *(B, D)* P5 ventral view (pits on dorsal side); *(C)* P2; *(E)* antennule; *(F, G)* details of coupling denticles and dactylus. Female: *(H)* rostrum (ventral). Scale bar: A = 0.1 mm. B, C, E, H = 0.14 mm. F = 0.06 mm. G = 0.08 mm.

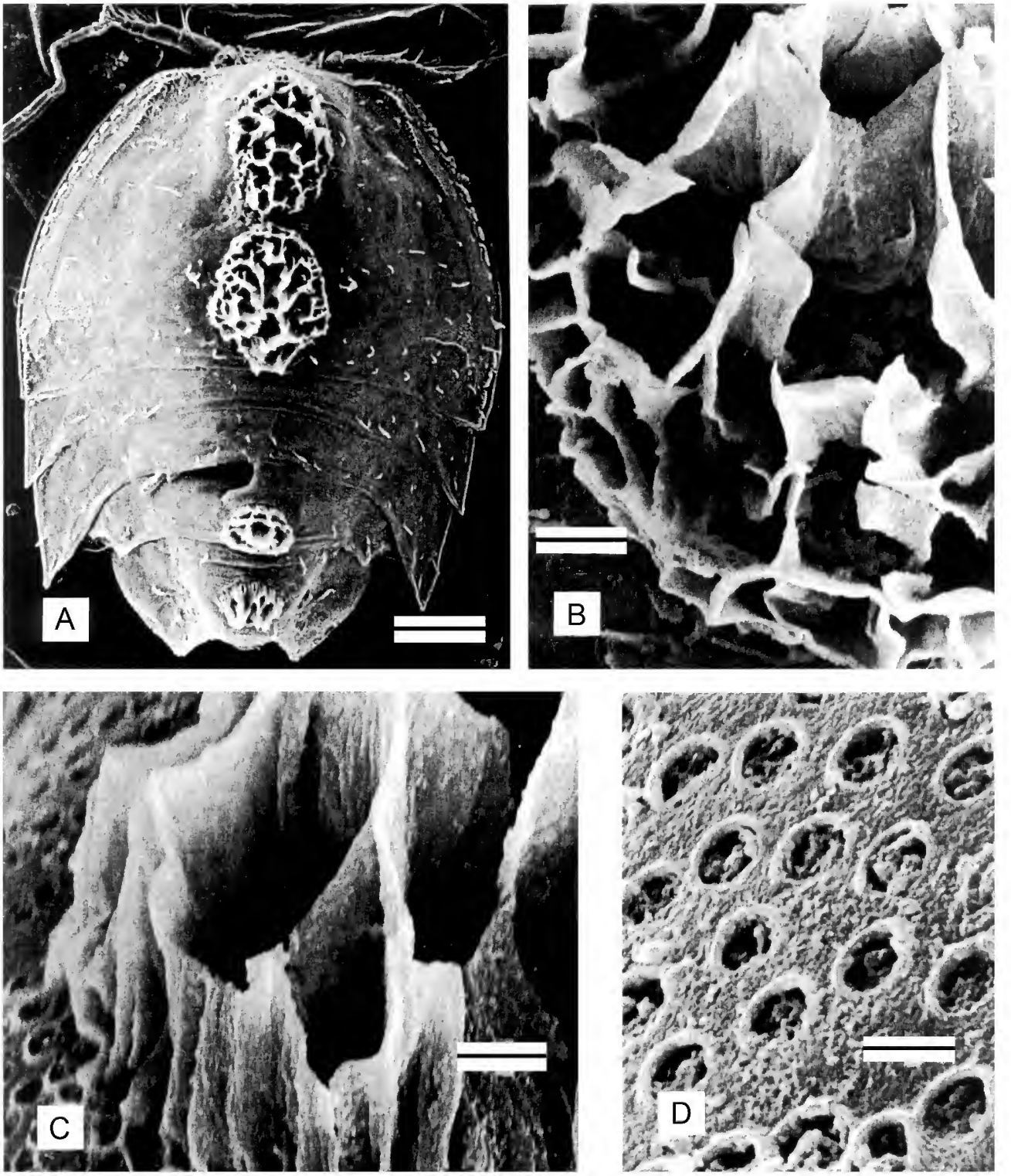

Plate 1. Scanning electron micrographs of *Cereudorsum verrucosum*. *(A)* adult female (dorsal, note caudal rami and P5 limbs missing); *(B, C)* honeycomb-like cuticle; *(D)* dorsal pits. Scale bar: A = 0.13 mm. B = 0.016 mm. C = 8.5 µm. D = 3.2 µm.

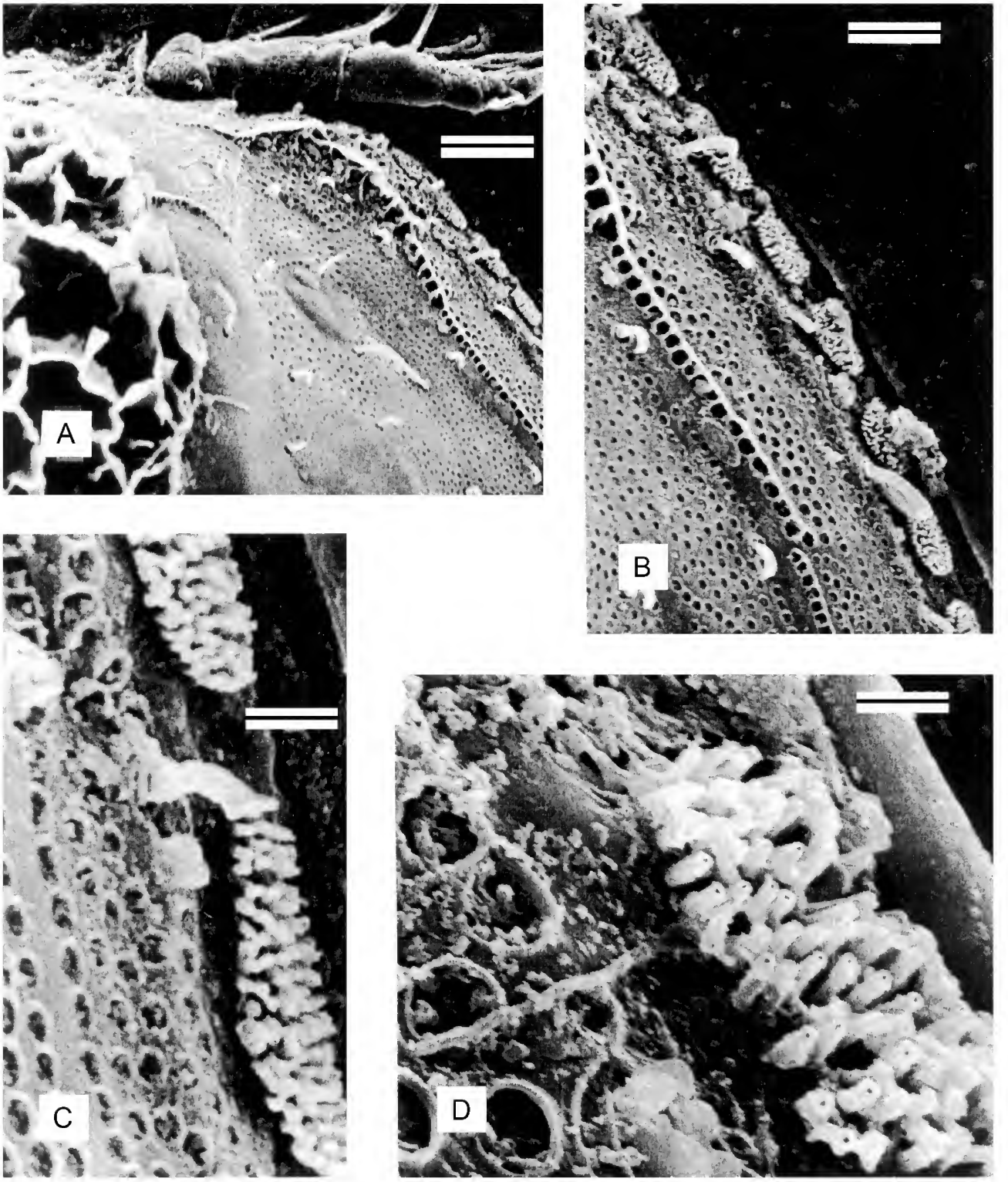

Plate 2. Scanning electron micrographs of *Cereudorsum verrucosum*. *(A)* right "shoulder" region of female cephalosome; *(B)* border of cephalosome showing blocks of micro-tubules; *(C, D)* detail of microtubules. Scale bar: A = 0.045 mm. B = 0.022 mm. C = 6.4 µm. D = 3.2 µm.

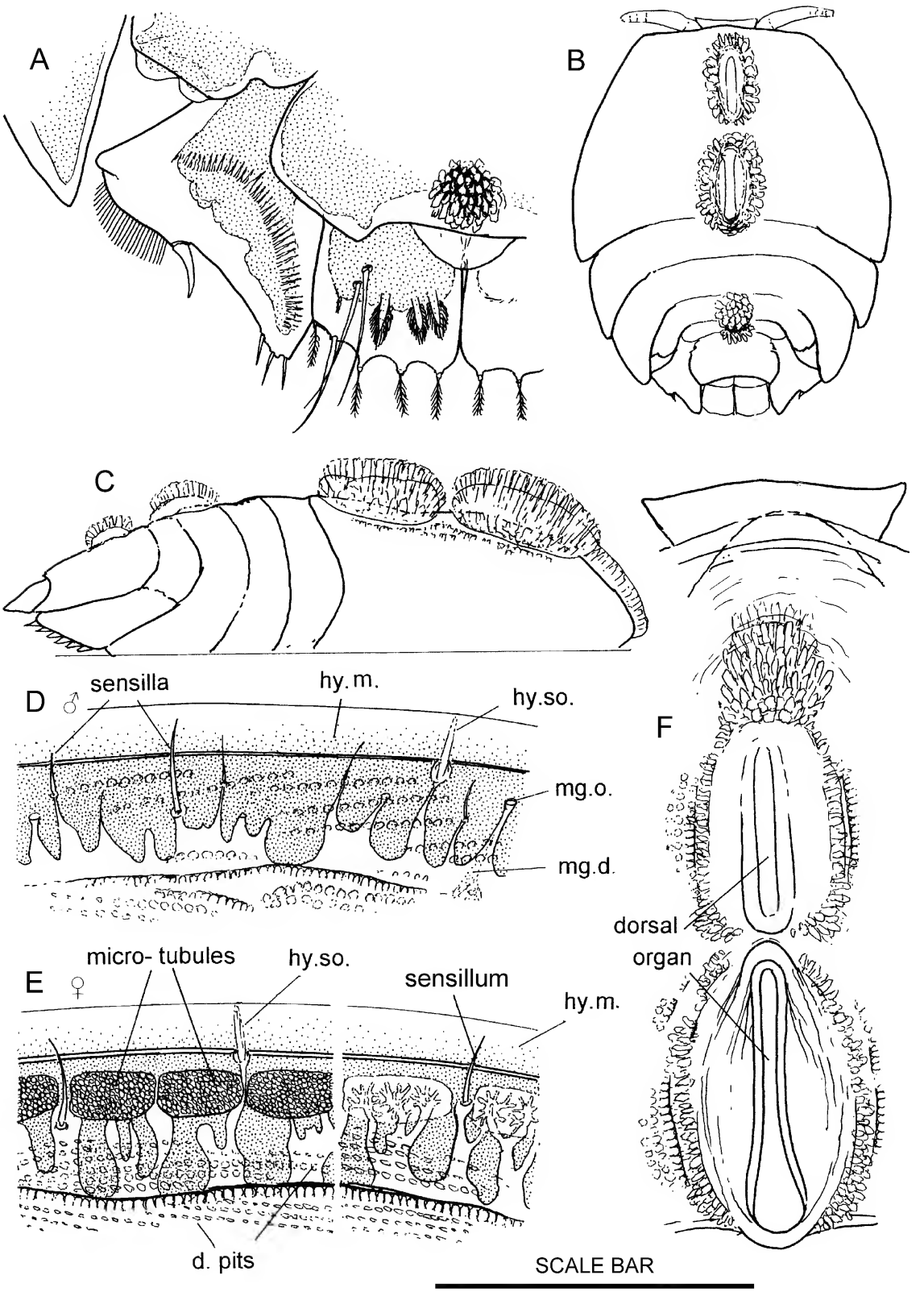

Figure 4. *Cereudorsum verrucosum* sp. nov. *(A)* P5 and caudal ramus of pharate stage V female copepodid, showing difference in type of setae between adult and juvenile; *(B)* stage V female copepodid; *(C)* lateral view of adult male; *(D)* border of male cephalosome, note absence of micro-tubules (*hy.m.* hyaline membrane; *hy.so.* hyaline sense organ; *mg.d.* duct of marginal gland; *mg.o.* opening of marginal duct); *(E)* border of female cephalosome (left superficial focus showing micro-tubules, right deep focus showing branched ducts of marginal glands, lettering as for *D*; *d.pits*, dorsal pits); *(F)* dorsal organs and cuticular honeycomb of stage V copepodid (dorsal view). Scale bar: A, F = 0.14 mm. B = 0.55 mm. C = 0.35 mm. D, E = 0.08 mm. F = 0.14 mm.

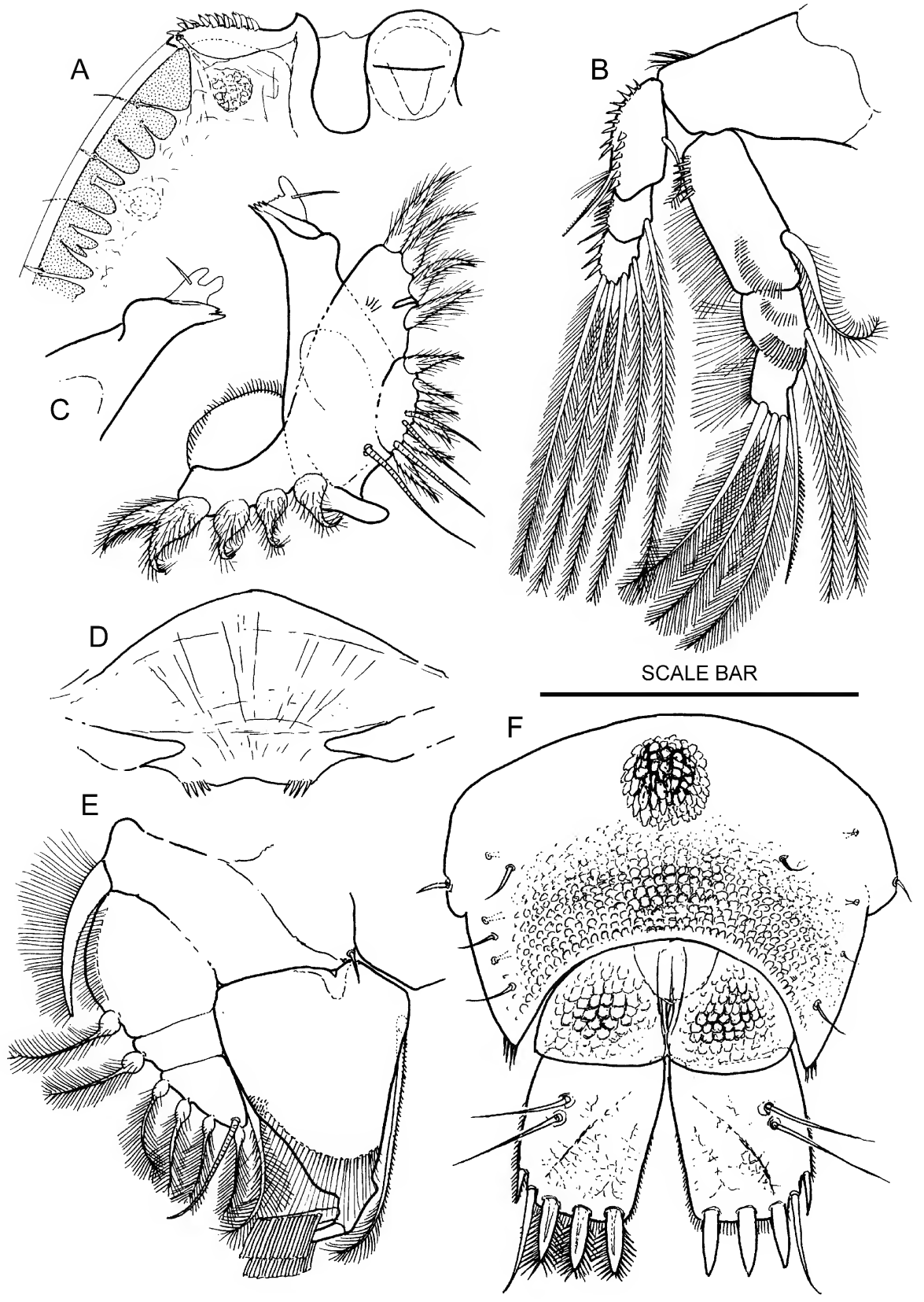

Figure 5. *Cereudorsum verrucosum* sp. nov. Male: *(A)* rostrum and "shoulder" (ventral); *(F)* genital double-somite and caudal rami. Female: *(B)* P2; *(C)* mandible and molar process; *(D)* labrum; *(E)* P1. Scale bar: A = 0.22 mm. B, C = 0.18 mm. D = 0.1 m.m. E = 0.15 mm. F = 0.14 mm.

Biometric data. *Females* (N = 6): maximum length (L_{max}) mean 0.92 mm, range 0.90–0.98 mm, body length (L_{urs}) mean 0.85 mm, range 0.82–0.86 mm; cephalosome width (W) 0.65 mm, range 0.63–0.66 mm, length 0.47 mm; rostrum width (R) 0.13 mm; genital double-somite width 0.35 mm, length 0.20 mm; caudal ramus width 0.08 mm (¾ down ramus), length 0.16 mm.

Ratios: L_{urs}/W1.3, L_{max}/W1.4, cephalosome 55% of L_{urs}, W/R5.0; genital double-somite w/l 1.75, width 54% of cephalosome, anterior lobe 77% of lateral border, posterior lobe 23% of lateral border; caudal ramus 19% of L_{urs}, l/w 2.0, Hicks' index for α 86%, for β 60%.

Males (N =8): maximum length (L_{max}) 0.72 mm, range 0.70–0.76 mm; cephalosome width (W) 0.55 mm, range 0.49–0.57 mm, length 0.32 mm; rostrum (ventral) 0.07 mm; caudal ramus width 0.055 mm, length 0.065 mm; antennule length (fully extended) 0.20 mm; spermatophore 0.18 × 0.04 mm.

Ratios: L_{max}/W 1.3, cephalosome 43% of L_{max}, W/R 7.8; caudal ramus l/w 1.15, Hicks' index for α 68%, for β 60%; antennule 27% of body length, antennule segment 2 34%, segments 3+4 34%, dactylus 24%, aesthetasc 78% of antennule length; spermatophore 25% of L_{max}.

Description. *Adult females* (Fig. 1A): colourless or very pale amber, heavily sclerotized regions brown. Body outline elliptical, truncated anteriorly with convex bulge above rostrum, rostrum (Fig. 3H) partly obscured by anterior bulge. Hyaline border clear, 12–14 µm wide. Rows of conspicuous pits (3 µm) surrounded by rim of thickened cuticle ornament dorsal surface of cephalosome, metasome, genital double-somite and P5s (Plate 1D, p. 172), conspicuous cuticular ridge runs parallel to edge of cephalosome and medial to the blocks of microtubules (Fig. 1A; Plate 2B, p. 173). Numerous (> 100) sensilla form a regular pattern on the dorsal surface of the cephalosome, metasome segments and genital double-somite (Plate 1A, p. 172; Fig. 1C). Some resemble setae, but most are short tubular structures with a basal collar that project through holes in the cuticle (Plate 2B,C, p. 173). Two massive cuticular outgrowths resembling honeycomb 30–50 µm high (Fig. 1A, 4C; Plate 1A,B,C, p. 172) are present on dorsal midline of cephalosome. Individual cells range from 5–40 µm in diameter and have very thin walls (< 0.5 µm). Similar, but smaller, cuticular outgrowths are present on metasome 3 and genital double-somite. On either side of anterior half of cephalosome there are eleven blocks of microtubules close to hyaline border (Figs 1A, 4E left side; Plate 2A–D, p. 173). Each block contains 80–100 tubules and each tubule is 0.75 µm in diameter, 2.5 µm high and has a lumen 0.15 µm in diameter (Plate 2D, p. 173). Labrum without ridge plates, posterior edge with three or four setules at lateral corner (Fig. 5D). Genital double-somite about half width of cephalosome (Fig. 1C, note that width is distorted in drawing by pressure of coverglass), a distinct notch marks boundary between anterior and posterior lobes, one sensillum mid-way along edge of anterior lobe, posterior lobe about ¼ length of genital double-somite, (in normal view posterior lobe appears pointed, but when laid flat it is rounded, Fig. 1C), setules on posterior lobe smaller than those on anterior lobe (Fig. 1E). Dorsal surface pitted, many seta-like sensilla present plus area of honeycomb cuticle in midline. Posterior arch deep, surrounds about ½ of caudal furca. Genital opening straight (Fig. 2I). Metasome segment 4 with fimbriate setules on posterior edge of sternum. Caudal rami broad, elongate (Fig. 1F), medial edge straight with setules down length, lateral edge slightly convex with few setules distally. Seta T1 small pinnate, deeply recessed, posterior border slightly convex with three very large pinnate setae (T2, T3 and T4) evenly spaced (Fig. 1D). Dorsal surface with two longitudinal ridges and some net-like markings, α and β setae very long (about ½ length of ramus).Seta on first segment of antennule pinnate. Structure and setation of mouthparts and ambulatory limbs typical of family. Basis of antenna with row of triangular setules (Fig. 2A), exopod with six plumulose setae, segment 2 of endopod with three lateral setae, geniculate setae plain, claw comb-like. Mandible with small group of setules on anterior lobe (Fig. 5C). Maxillule with single bulbous seta on exopod (Fig. 2B). Maxilla as in Fig. 2D. Maxilliped coxae do not meet in midline (Fig. 2C), coxa with fimbriate border, fimbriate process greatly reduced in size and represented by a bunch of fine fimbriate setules (Fig. 2H). Endopod of P1 with small area of denticulate setules at lateral end of fimbriate crescent (Fig. 5E). P2 endopod with strong proximal setules on segment 1, serrulate spinous seta on segment 3 ⅔ length of endopod (Fig. 5B). Serrate spinous seta on segment 2 of P3 endopod (Fig. 2F) shorter than endopod (0.7:1), large serrate spinous seta on segment 3 very much longer than endopod (1.7:1). P4 endopod segment 1 without internal seta (Fig. 2G), seta on segment 2 and first internal seta of segment 3 thin, straight spinous. Exopod of P5 lanceolate (Fig. 2E), dorsal surface with rows of pits, one sub-terminal seta and two apical setae, border setules long (25 µm). Females carry 10 eggs per brood.

Adult males (Fig. 1B). Outline of cephalosome a sharply truncated hemi-ellipse, convex in midline above rostrum, rostrum rounded (Fig. 5A), lateral angle of antennule sockets project forward, shoulder with epaulet and several cuticular serrations (in ventral view, Fig. 5A), hyaline border starts at epaulet. No microtubules on border of cephalosome (Fig. 4D), ducts from marginal glands open individually dorsal to hyaline border. Colour, pits, ridges, sensilla and massive dorsal cuticular honeycomb as described for female. Caudal rami rectangular (Figs 3A, 5F), lateral edge convex, with setules at posterior end, posterior border slightly convex with fine setules, setules down medial edge, dorsal surface with longitudinal ridge and net-like markings, α and β setae very long (almost length of ramus), inserted very close together about ⅓ way down ramus. Terminal seta T1 small, pinnate, recessed at lateral corner, T2, T3 and T4 large pinnate setae evenly spaced. Antennule (Fig. 3E) without denticle on segment 3, four or five closely grouped finger-like processes (not cuticular denticles) on segment 4 (Fig. 3F), dactylus shorter than segment 3+4, with small hook at end of segment 5 (Figs, 3E, G), aesthetasc long (about ¾ length of antennule), divided into three sections by two constrictions. Terminal segment of P2 endopod with two plumose setae and one serrulate spinous seta (Fig. 3C). Segment 1 of P4 endopod without internal seta, setae on segments 2 and 3 plumose (not spinous). P5 exopod acutely trapezoid (apical angle 50°) with rows of pits on dorsal surface (Fig. 3B), first (lateral) seta with five strong ventral setules, each terminal seta with two or three setules at its base (Fig. 3D).

Remarks. This species is remarkable for a number of unusual features. Nothing corresponding to the dorsal organs and their cuticular outgrowths has been found on any other member of the Porcellidiidae. They do not appear to be derived from any ancestral or pre-existing structure. They first appear on stage III copepodids, but after metamorphosis to adult the trough is completely obscured by the massive honeycomb cuticle. These structures occur on both sexes and first appear on stage III copepodids in a simple form. They are best interpreted from juvenile stages because the mass of cuticular honeycomb is shorter and does not obscure the dorsal organs (Fig. 4B). The dorsal organ on stage V copepodids appears as a longitudinal trough with thickened rim (Fig. 4F). This is surrounded by a clear oval area which is bounded by a ridge and pits, similar to the ridge parallel to the edge of the cephalosome but greatly extended in height to form the folds of the cuticular honeycomb. In adults the honeycomb is massive and completely obscures the dorsal trough (Fig. 1A, 4C; Plate 1A, p. 172). The function of the dorsal organ and cuticular honeycomb is not known.

Ducts from marginal glands of male animals open individually close to the hyaline border as in other porcellidiid species (Fig. 4D), but similar ducts are not found in female animals in the region of microtubule blocks (Fig. 4E, left hand side). From the body cavity passages run through the thickened cuticular border of the cephalosome and end in fine branches under the blocks of microtubules (Fig. 4E, right hand side). It is assumed that secretions from the marginal glands exit through the microtubules. Blocks of microtubules are not found on juvenile animals, but first appear at the moult from stage V copepodid to adult female.

The caudal rami of copepodid stages bear typical thin pinnate setae. The large pinnate setae with hollow shaft do not appear until the final moult to the adult stage (Fig. 4A shows a pharate stage V female copepodid with both juvenile and adult terminal setae). Unlike the clavate setae of *Clavigofera*, the pinnae do not originate from a thin lateral expansion of the shaft, but from the shaft itself.

The male antennules are also unique for they have finger-like structures on segment 4 that appear to take the place of coupling denticles found on all other species. They may perform the same function of increasing friction during mate guarding behaviour.

Etymology. The specific name refers to the wart-like appearance of the dorsal organs (L. *verruca* = a wart).

Distribution. *Cereudorsum verrucosum* has only been found on partly decomposed *Ecklonia radiata* in muddy water at the entrance to Gunnamatta Bay, Port Hacking. This is unusual for it is very rare to find porcellidiids on rotting algae and only one or two species can tolerate muddy water. Nearly all the animals in the sample are covered with diatoms, suctorian protozoa, moulds and sand particles, which make critical observation of detail difficult. The type series, Cr34. 2/77, contained 82 ♀♀, 54 ♂♂ (8 coupled to female copepodids) and 8 copepodids. V. A. Harris 1977.

Genus *Geddesia* gen. nov.

Porcellidium.—Geddes, 1968: 11.

Type species. *Geddesia quadrata* sp. nov.

Diagnosis. Male antennule unique, no denticle or comb on segment 3, two serrate denticles and two spherical structures on segment 4; female cephalosome truncated anteriorly, male deeply concave anteriorly; hyaline border to lateral edge; no dorsal organ with cuticular honeycomb; no ridge plates or setules on labrum; female caudal ramus pentagonal, medial corner 90°, posterior border between T2 and T4 straight, T3 absent; maxillule endopod with six setae; coxae of maxillipeds touch in mid-line; female P5 exopod without ventral expansion, not truncated posteriorly, dorsal and apical setae not pinnate.

Species composition. *Geddesia trisetosa* (Geddes, 1968) comb. nov.; *Geddesia quadrata* sp. nov.

Etymology. The genus is named after Dr D. C. Geddes.

Remarks. The genus is defined on the unique structure of the male antennule, number of setae on maxillule endopod and absence of T3 seta on caudal ramus (compare with *Mucrorostrum, Clunia* and *Brevifrons*).

Geddes' *Porcellidium trisetosum* is included here on the assumption that its maxillule exopod has six setae (Geddes states that "…mouthparts like those of *P. viride* (Philippi) as described by Sars (1911)", this implies six setae on the maxillule, Geddes (1968: 11).

The genus is known from Bahamas and Great Barrier Reef, Australia.

Key to species of *Geddesia*

1 Male P2 endopod with two terminal setae. Male T2 and T4 on caudal ramus short (< ⅕ ramus width). Gap between T2 and T4 > ¾ of maximum width of male caudal ramus. Colour yellow. (Plate 1D, p. 172) ..... *G. quadrata* sp. nov.

—— Male P2 endopod with three terminal setae. Male T2 and T4 on caudal ramus long (> ½ ramus width). Gap between T2 and T4 ½ maximum width of caudal ramus. Colour brown-red ..... *G. trisetosa* (Geddes, 1968)

Geddesia quadrata sp. nov.

Figs 6–9

Type material. HOLOTYPE, adult male, length 0.86 mm, P81221; ALLOTYPE, adult female, length 1.06 mm, P81222 (both mounted on slide), deposited at AM, Sydney. PARATYPE female mounted on slide and deposited at NHM, London. All collected from seagrass (*Zostera* sp?), Green Island, Great Barrier Reef, Queensland, Australia (16°41'S 45°56'E), V. A. Harris, 1973.

Diagnosis. Female cephalosome hemi-ellipse sharply truncated, anterior edge straight, clear area (lens) above rostrum; male cephalosome deeply concave anteriorly; α and β setae on male caudal ramus and terminal setae T1, T2, T4, all very short (< ¼ width of ramus); area of denticulate setules on P1 endopod resemble maize corn cob; male P2 with two terminal setae on endopod; falciform ventral ridge on female P5 exopod with deep posterior (apical) notch; female length 1.06 mm, colour yellow.

Biometric data. *Females* (N = 4): maximum length (L_{max}) 1.06 mm, body length (L_{urs}) 0.98 mm; cephalosome width (W) mean 0.75 mm; rostrum width 0.16 mm; genital double-somite width 0.33 mm, length 0.22 mm; caudal ramus length 0.15, width 0.08 mm.

Ratios: L_{urs}/W 1.3, W/R 4.7; genital double-somite w/l 1.5, arch 50% of length; caudal ramus 15% of L_{urs}, l/w 1.8, Hicks' index for α 80%, β 50%.

Males (N = 3): length (L_{max}) 0.86 mm [0.90 mm*], body length (L_{urs}) 0.81 mm [0.85 mm*]; cephalosome width 0.70 mm, length 0.47 mm [0.50 mm*]; antennule fully extended 0.21 mm; spermatophore 0.21 × 0.09 mm. [* = Measured from shoulder. Due to the deeply concave anterior border of the male cephalosome, the length measured from the rostrum is very much shorter.]

Ratios: L_{max}/W 1.2 [1.28 mm] cephalosome length 55% of L_{max}; caudal ramus l/w 1.0; antennule 23% of L_{max}, segment 3+4 38%, dactylus 27% of antennule length; spermatophore 25% of L_{max}.

Description. *Adult females* (Fig. 6A; Plate 1D, p. 172): colour lemon yellow, cephalosome hemi-ellipse strongly truncated anteriorly with small epaulette at shoulder, rostrum prominent (Fig. 6B, C) with clear lens-like structure dorsal to rostrum. Dorsal pits very small (2 µm) near edge of cephalosome, hyaline border clear, 15 µm wide (Fig. 7C). Labrum without setules or ridge plates. Genital double-somite (Fig. 7D) narrow (less than ½ width of body), very small notch marks boundary between anterior and posterior lobes (Fig. 7F marked with *), posterior lobe about ¼ length of anterior lobe, acutely pointed posteriorly, lateral edge with very short border setules, arch less than ½ length of genital double-somite. Genital opening (Fig. 6F). Caudal ramus (Fig. 6E) pentagonal, widens posteriorly, maximum width ⅔ down ramus, dorsal surface with fine reticulation. Bevelled edge with setules, posterior edge straight, ¾ of maximum width, 90° to medial edge, posterior border setules conspicuous. Beta seta half way down ramus, T1, and γ close together near posterior end of bevelled edge, T3 absent, T4 small at medial corner. Structure and setation of mouthparts and ambulatory limbs typical of family. Antenna (Fig. 7A, B) with fine setules along edge of basis and endopod segment 1, exopod with five plumulose setae and one serrulate spinous seta, geniculate setae on endopod segment 2 with plain terminal section, claw comb-like. Setae on mandible endopod unusually long (Fig. 7D). Maxillule with six setae on endopod. Claw on maxilla with distal edge comb-like (Fig. 7H). Maxilliped (Fig. 7E). P1 (Fig. 8F), exopod segment 1 with single row of denticles parallel to edge, endopod segment 1 short, broad (w/l = 0.9) with elongate patch of denticulate setules that resemble maize corn cob at lateral end of fimbriate crescent. Setules along external edge of segment 1 on P2, P3 and P4 exopods unusually strong (Fig. 8A, C, D). Serrate spinous seta on segment 2 of P3 endopod strong, almost as long as endopod (0.9:1), large serrate spinous seta on segment 3 longer than endopod (1.35:1, Fig. 8A). Seta on endopod of P4 segment 2 and internal seta of segment 3 strong serrulate spinous setae ½ length of endopod (Fig. 8D). P5 exopod (Fig. 6G) lanceolate, apex rounded (not acute), apical end of ventral falciform ridge terminates in notch (Fig. 7G), two dorsal and one apical seta present (not pinnate), P5s extend beyond genital double-somite but are separated by full width of caudal rami. Females carry six eggs.

Adult males (Fig. 9A), colour lemon yellow, cephalosome truncated hemi-ellipse, posterior half of body semi-circular. Anterior of cephalosome strongly concave, convex medial prominence above rostrum with clear, lens-like, structure in rostrum (Fig. 9D), small epaulette present (Fig. 9B). Dorsal pits and hyaline border as for female. Caudal ramus (Fig. 8B) square (l/w = 1), dorsal surface with reticulate markings, lateral edge slightly convex with border setules along posterior half, α and β setae about ¼ width of ramus or less, β seta half way down ramus. Medial corner 90° with T4 at corner, setae T1 and γ recessed at lateral corner (no bevelled edge), T3 absent, posterior border straight with conspicuous row of setules, distance between T2 and T4 80% of ramus width. Antennule (Figs 9E, F) without denticle or comb on segment 3, prominent peg-like ventral process present (marked * on figures), segment 4 with two small serrated denticles and two bulbous structures (Fig. 9E, F). Dactylus cylindrical, as long as segment 3+4.Two plumose terminal setae on P2 endopod (Fig. 8E), setae on P4 endopod plumose (not spinous). P5 exopod (Fig. 9C) trapezoidal, lateral seta same size and shape as five terminal setae, row of 20 ventral setules, no setules at base of terminal setae. Spermatophore ¼ length of body.

Etymology. The specific name refers to the straight posterior border of the caudal ramus which makes an angle of 90° with the medial edge, (L. *quadratus* = made square).

Remarks. The female animal described by Geddes (1968) as *Porcellidium trisetosum* lacks the T3 seta on its caudal ramus and the female cephalosome is truncated anteriorly: two features that exclude it from the genus *Porcellidium*. The male antennule is not described, but the maxillule is stated to be the same as Sars (1904) described for *P. fimbriatum*, which has six setae on the endopod. Therefore, Geddes' *trisetosum* fits the diagnosis of *Geddesia* and should be moved to that genus as *Geddesia trisetosa* (Geddes, 1968) comb. nov.

The latter differs from *G. quadrata* in the following features: size of female (L_{max} 0.78 mm), colour (red-brown), male P2 endopod with three terminal setae, female Hicks' index for α 70%, length of spinous setae on female P4 endopod as long as endopod, male P5 with setules at base of each terminal seta.

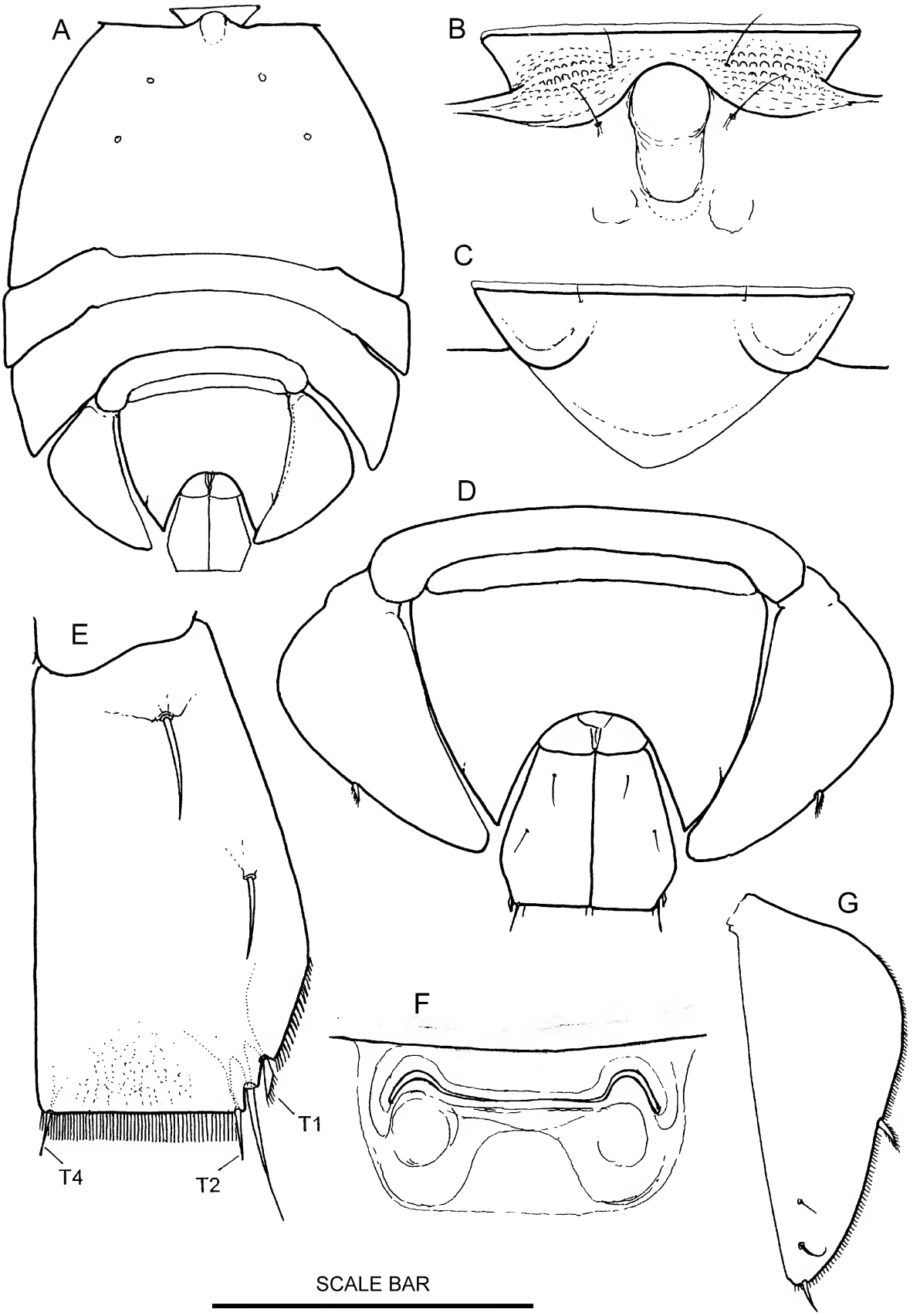

Figure 6. *Geddesia quadrata* sp. nov. Female: *(A)* adult; *(B, C)* rostrum (dorsal, ventral); *(D)* urosome and caudal furca; *(E)* caudal ramus; *(F)* genital opening; *(G)* P5 (dorsal). Scale bar: A = 0.6 mm. B, C = 0.13 mm. D = 0.3 mm. E = 0.1 mm. F = 0.08 mm. G = 0.23 mm.

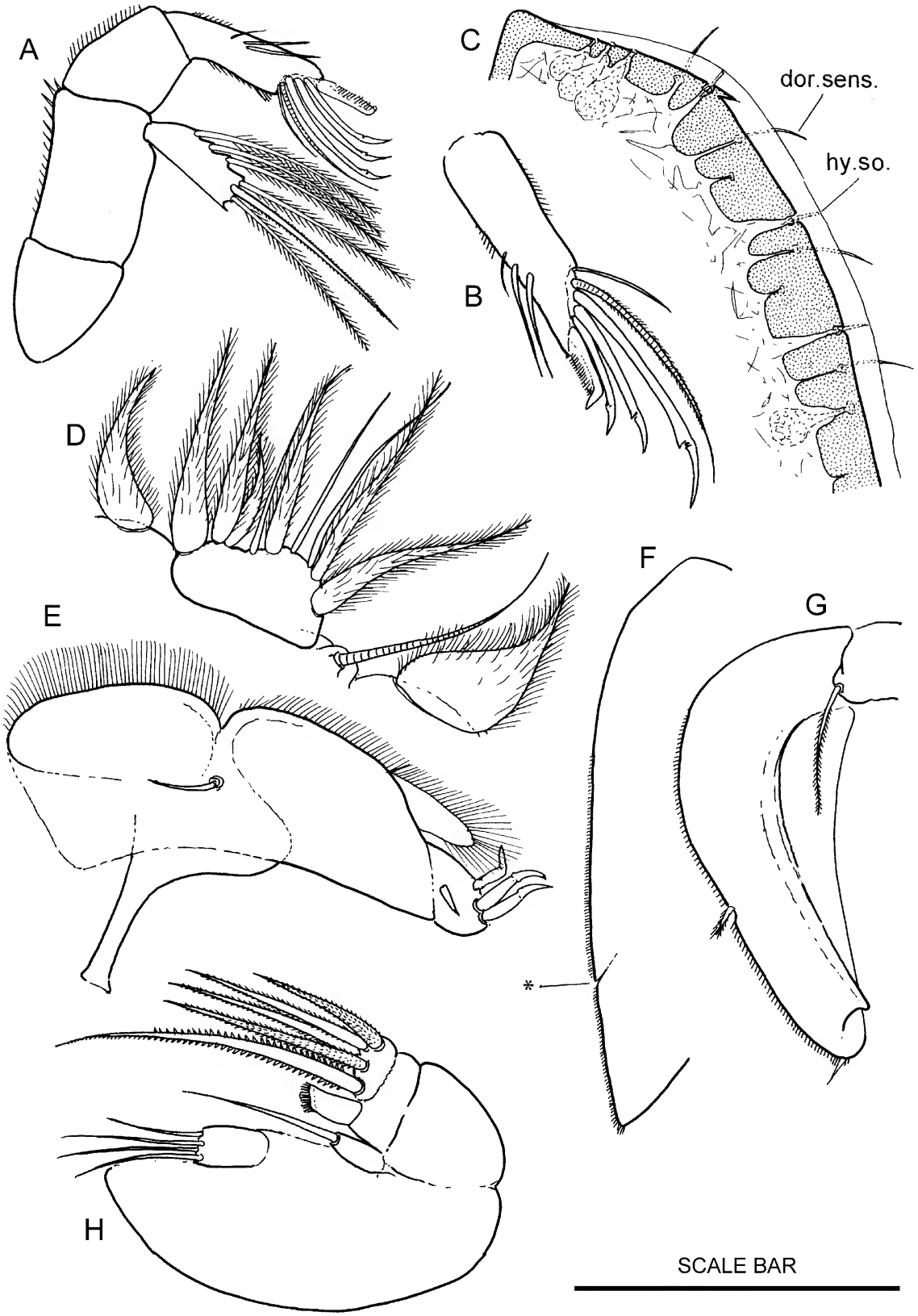

Figure 7. *Geddesia quadrata* sp. nov. Female: *(A, B)* antenna; *(C)* edge of cephalosome (*dor.sens.* dorsal sensillum; *hy.so.* hyaline sense organ); *(D)* mandible endopod; *(E)* maxilliped; *(F)* edge of urosome (* notch); *(G)* P5 (ventral); *(H)* maxilla. Scale bar: A, C, F = 0.14 mm. B, D, E, H = 0.1 mm. G = 0.37 mm.

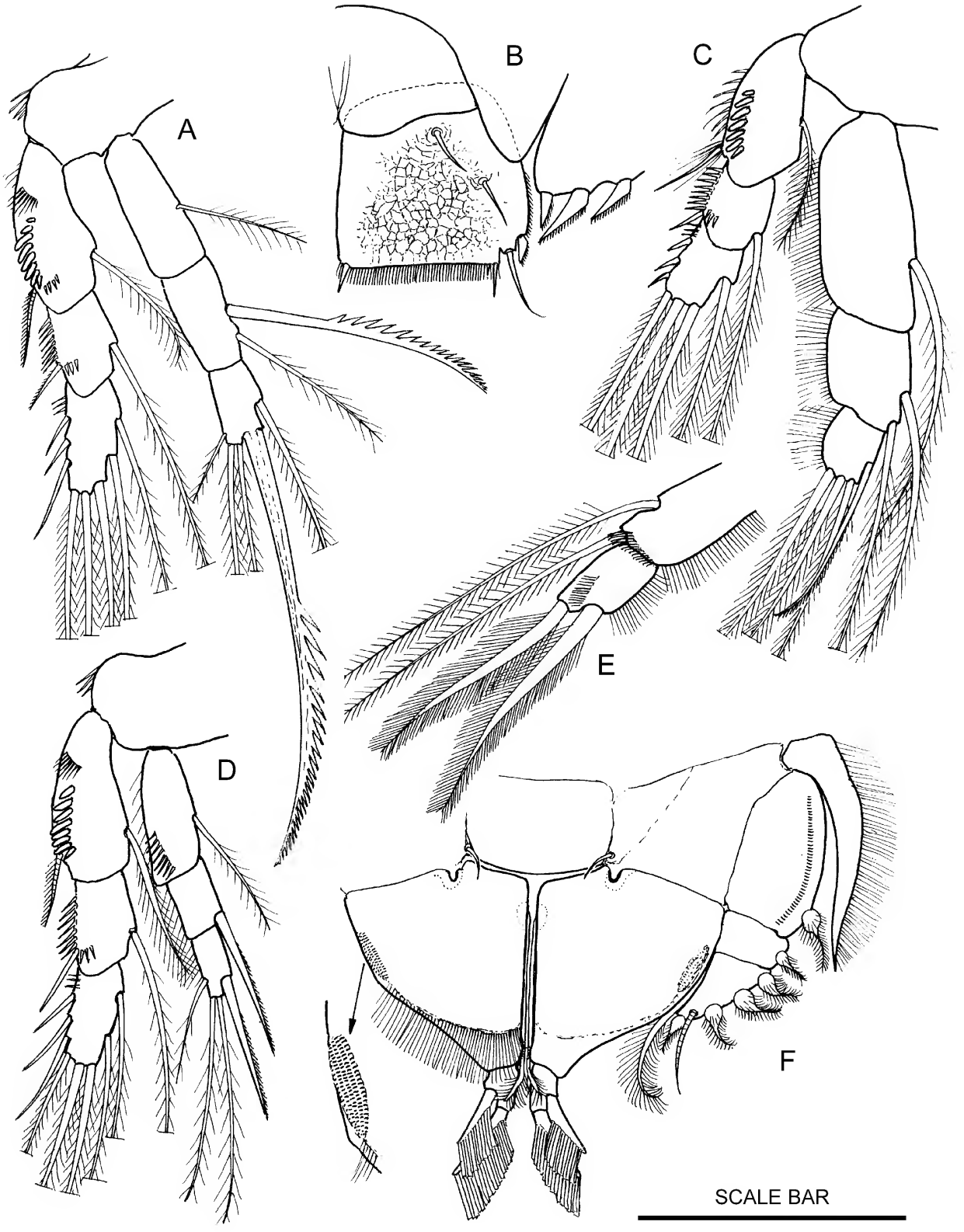

Figure 8. *Geddesia quadrata* sp. nov. Female: *(A)* P3; *(C)* P2; *(D)* P4. Male: *(B)* caudal ramus; *(E)* P2 endopod terminal setae; *(F)* P1. Scale bar: A, C, D = 0.14 mm. B, E = 0.1 mm. F = 0.15 mm.

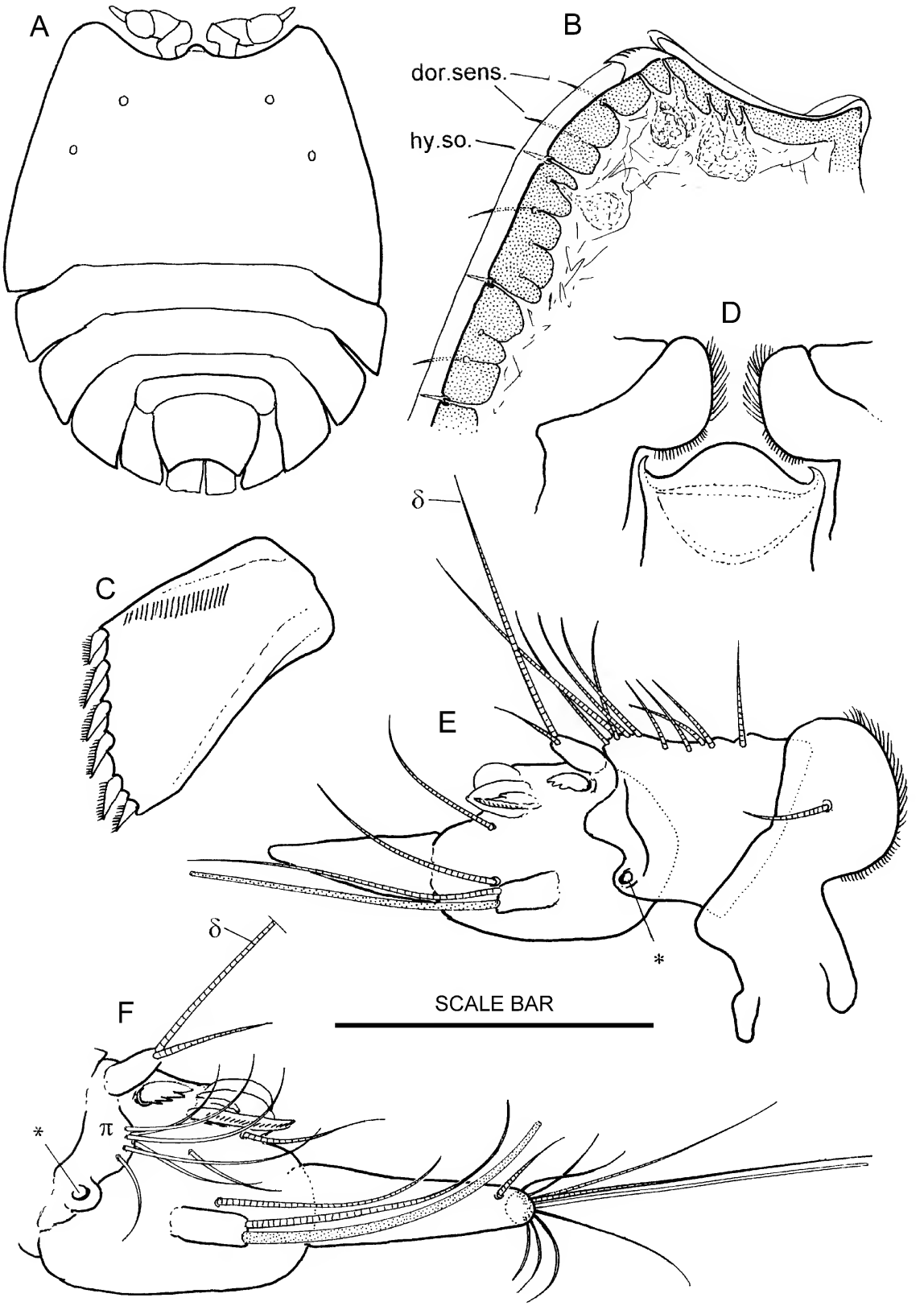

Figure 9. *Geddesia quadrata* sp. nov. Male: *(A)* adult; *(B)* edge of cephalosome; *(C)* P5 (ventral); *(D)* rostrum (ventral); *(E)* antennules; *(F)* details of coupling denticles (* ventral process or peg). Scale bar: A = 0.6 mm. B, C, D = 0.14 mm. E = 0.1 mm. F = 0.08 mm.

Distribution. Type series collected from sea grass *Zostera capricornia* on the reef side of Green Island, Cairns, Great Barrier Reef, Australia, 6 ♀♀, 2 carrying eggs, 8 ♂♂, 2 juveniles, V. A. Harris, 1973. Geddes' animals come from the Bahamas.

Genus *Clunia* gen. nov.

Type species. *Clunia cocosensis* sp. nov.

Diagnosis. Maxillule endopod with only one seta;female cephalosome not truncated; hyaline border with sensilla at lateral edge of cephalosome; no dorsal organs with cuticular honeycomb; no ridge plates on labrum; no lateral striations to anterior lobe of female genital double-somite; female caudal ramus pentagonal, median corner 90°, posterior border straight, T3 absent; coxae of maxillipeds touch in midline; no ventral expansion to female P5 exopod.

Species composition. *Clunia cocosensis* sp. nov., is the only species currently known. Recorded from the Indian Ocean.

Etymology. The genus is named *Clunia* after John Cluniess-Ross who settled on the Cocos (Keeling) group of islands in 1827.

Remarks. The shape of the caudal ramus and absence of T3 resemble *Geddesia* and *Mucrorostrum*, but the presence of only one seta on the maxillule endopod (in contrast to six on the former and two on the latter) and the endite formula are unique features that justify erection of the genus *Clunia*. No male specimen is available for male characters that would confirm this decision.

Clunia cocosensis sp. nov.

Figs 10–11

Type material. HOLOTYPE adult female, length 1.06 mm, P81219; PARATYPE specimens (adult female and dissected female on slide) P81220, deposited at AM, Sydney. All collected from Cocos (Keeling) Islands, Indian Ocean, F. H. Talbot, 1979.

Diagnosis. Female cephalosome hemi-elliptical; dorsal cuticle almost devoid of pits; anterior lobe of mandibular palp long, without ventral setules, molar process modified as a scraper; single seta on maxillule exopod long, not bulbous, endopod with one seta, endite formula 2-3-1; first dorsal seta on P5 exopod close to lateral seta, apical seta pinnate.

Biometric data. *Females* (N = 3): maximum length (L_{max}) 1.03, 1.06, 1.09 mm, body length (L_{urs}) 0.94, 0.97, 0.99 mm; cephalosome width 0.65 mm; rostrum width 0.137 mm; genital double-somite 0.35 mm wide, 0.24 mm long: caudal ramus 0.12 mm long, 0.08 mm wide.

Ratios: L_{urs}/W 1.5, L_{max}/W 1.6, W/R 4.75; genital double-somite w/l 1.46; caudal ramus 12.4% of L_{urs}, caudal ramus l/w 1.5, Hicks' index for α 80%, for β 68%.

Description. *Adult female* (P81219, Fig. 10A). Natural colour unknown, specimens have light brown oil (?) droplets in body cavity. Rostrum not prominent, no lens in rostrum, dorsal pits small (3 μm) near edge of cephalosome, metasome segments and P5. Hyaline border clear, 12 μm wide. Genital double-somite (Fig. 11D) not broad, pointed posteriorly, lateral edge almost straight with no trace of division into anterior and posterior lobes, border setules absent except at apex, posterior arch less than ½ length of genital double-somite. Caudal ramus (Fig. 10G) pentagonal, maximum width about ⅔ down ramus, posterior border straight, 90° to medial edge. A diagonal ridge runs from proximal medial corner to insertion of T2 seta. Terminal setae T1, T2, T4 pinnate, T1 and γ recessed on beveled edge, T4 at medial corner, T3 absent. Terminal fringe of setules between T2 and T4 ⅔ maximum width of ramus. Structure and setation of mouthparts and ambulatory limbs typical of family. Exopod of antenna with five plumulose setae and one spinous seta, endopod segment 2 with three lateral setae, first terminal seta short, geniculate setae with plain end section, claw comb-like (Fig. 10E). Cutting edge of mandible molar process modified into trowel-like scraping organ without anterior seta or lappet (Figs 10B, C). Precoxa of maxillule elongate, endites bear 2-3-1 setae respectively, single plain seta on endopod and exopod (Fig. 10D). Maxilla (Fig. 11F) claw on endopod not broad or serrate, maxilliped (Fig. 10F). Conspicuous crescent of setules on segment 1 of P1 exopod (Fig. 11E), endopod with small but conspicuous triangle of setules at lateral end of fimbriate crescent. Spinous setules on external edge of P2, P3 and P4 exopod segments 1 and 2 appear to lie in a double row of about 9 + 9 setules (Figs 11A, C, G), segment 1 has a proximal row of nine fine setules and segment 3 has five or six setules. Serrated spinous seta on segment 2 of P3 shorter than endopod, large serrated spinous seta on segment 3 strong (Fig. 11C) longer than endopod (1.4:1). Spinous setae on P4 endopod segments 2 and 3 plain (Fig. 11G). P5 exopod lanceolate, not truncated posteriorly, two dorsal setae (first located very close to lateral seta—a position not known elsewhere in the Porcellidiidae) and one pinnate apical seta (Fig. 11B), border setules strong, P5s reach just beyond genital double-somite. One of the specimens has four large eggs in the brood chamber.

Adult male (no specimen available).

Etymology. Named from the Cocos Islands where the species was collected.

Remarks. The absence of a male animal renders the above description incomplete. The position of the first dorsal seta close to the lateral seta on the female P5 is unusual and has not been observed on any other member of the family.

Distribution. The four female specimens were collected at a depth of 4 m from dead coral encrusted with algae in a channel at the reef crest between Direction Island and Prison Island, Cocos (Keeling) Islands, Indian Ocean, F. H. Talbot, 8 Oct. 1979.

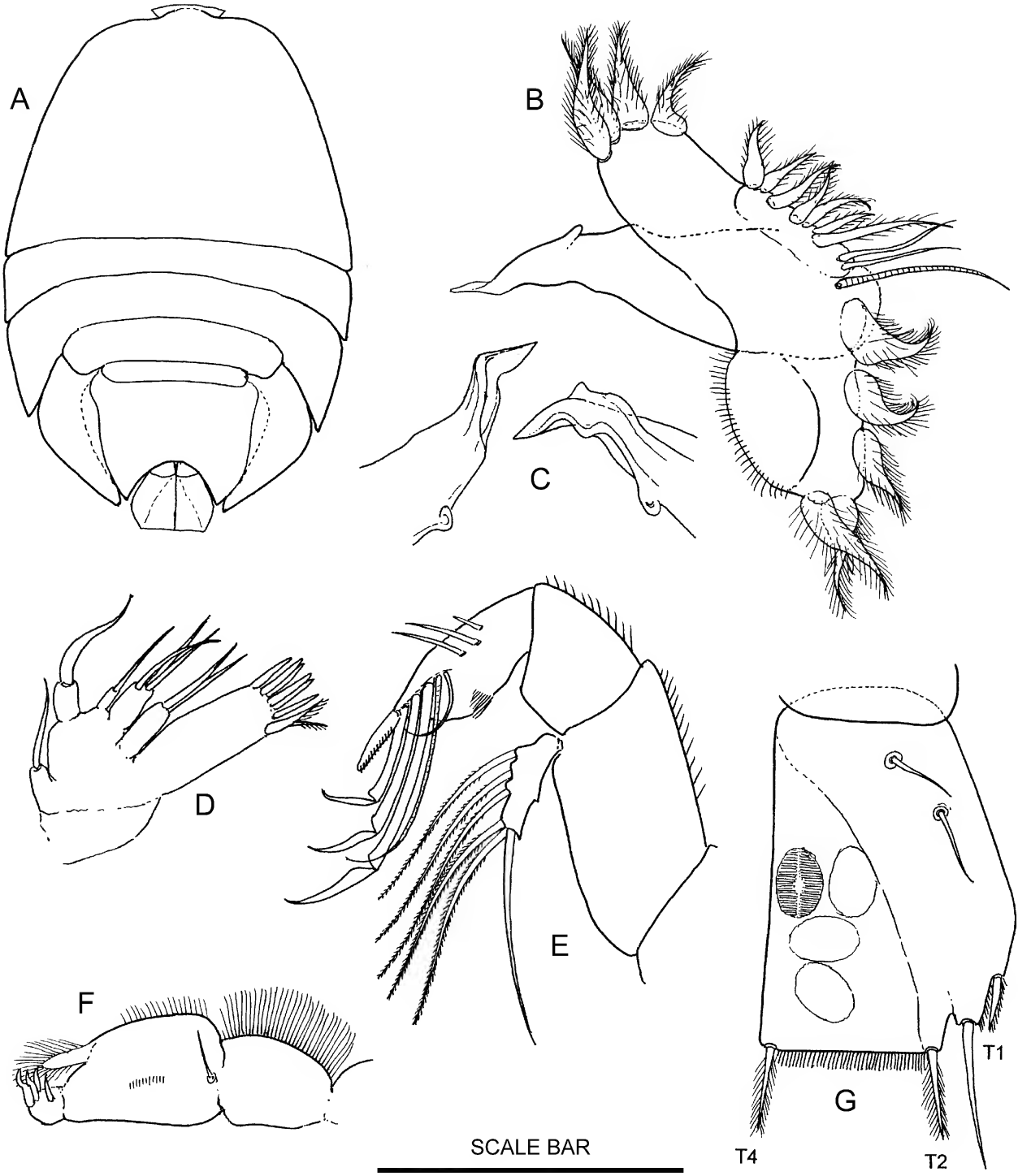

Figure 10. *Clunia cocosensis* sp. nov. Female: *(A)* adult; *(B, C)* mandible and detail of molar process; *(D)* maxilla; *(E)* antenna; *(F)* maxilliped; *(G)* caudal ramus (with diatoms on dorsal surface). Scale bar: A = 0.6 mm. B, C, D = 0.08 mm. E = 0.06 mm. F, G = 0.1 mm.

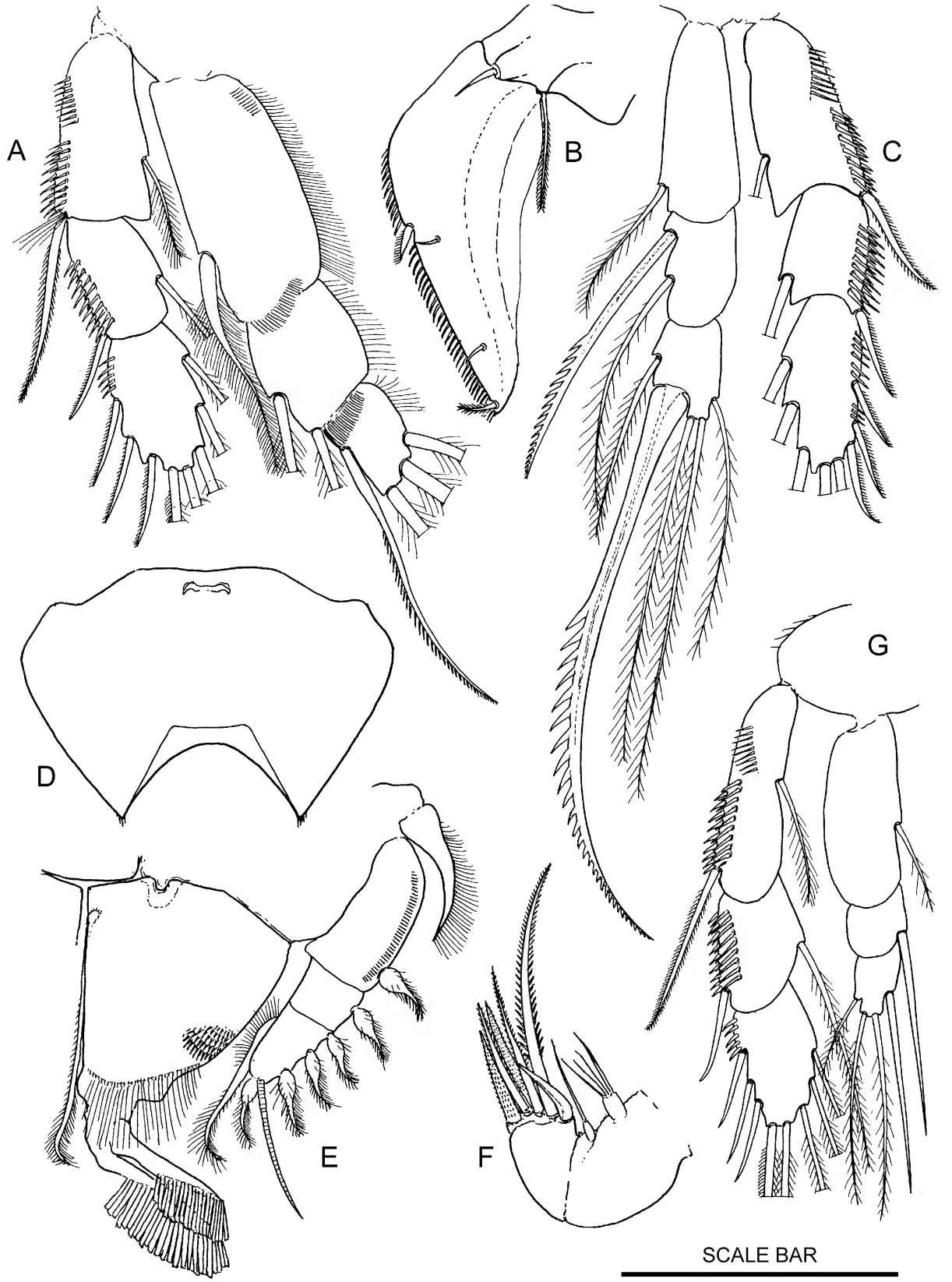

Figure 11. *Clunia cocosensis* sp. nov. Female: *(A)* P2; *(B)* P5 (ventral); *(C)* P3; *(D)* urosome; *(E)* P1; *(F)* maxilla; *(G)* P4. Scale bar: A, C, G = 0.1 mm. B = 0.23 mm. D = 0.3 mm. E, F = 0.08 mm.

Discussion

Reappraisal of the proposed genera and their validity

Sixteen genera have now been named, but not all of these have been accepted, either because the defining characters were not autapomorphic (Walker-Smith, 2001; Wells, 2007), or due to the fact that the type genus to the Porcellidiidae had not been clearly defined, resulting in a diverse assembly of very different species (Huys *et al*., 1996). The latter problem has been resolved with a definitive diagnosis for *Porcellidium* by Harris (2014a), but the first difficulty has not been addressed.

Wells (2007) objected that "… Although the ICZN neither precludes nor declares invalid taxa that are not in accord with Hennigian principles, they are now widely accepted as the ruling paradigms in systematics". Walker-Smith has pointed out that many of the genera were only defined on a unique combination of characters and not autapomorphies. However, Bodin (1997) points out that the diagnoses given "… of these genera are in accordance with the rules of the ICZN… ". It is necessary, therefore, to reconsider the grounds on which the disputed genera were based.

A careful re-examination of type material for all Australian and Japanese genera in the Porcellidiidae has been made to assess whether the unique features found were specific to only one species or to a closely defined group of species as autapomorphic characters defining a genus. The current data base contains detailed information on over 70 species. It shows certain features, such as shape of the cephalosome, caudal ramus, genital double-somite and structure of the male antennule, are extremely variable and may be useful species-specific characters. On the other hand, variation in a feature like the number of setae on the maxillule endopod, which is almost constant throughout the family, is more likely to be regarded as an autapomorphic character defining a genus. A number of other unique features, such as the brush pad of *Kensakia*, ventral hyaline membrane of *Tectacingulum* or the loss of terminal setae from the male P5 of *Synurus* are regarded as characters defining genera.

The result of this re-assessment is given in Table 1 where apomorphic and autapomorphic characters are listed for each genus except *Porcellidium* and *Acutiramus*. A total of 33 characters have been selected to define *Porcellidium*, all are present on the type species *P. viride* and appear to be plesiomorphic: none of them are considered autapomorphic. However, each of them are known to have a corresponding apomorphic state which is indicated in Table 1.

Remarks

Table 1 gives the main defining characters for each of the genera. *Porcellidium* is based on characters that are exhibited by *Porcellidium viride* and all species placed in that genus. Genera 3 to 16 are clearly defined by easily seen autapomorphic characters that separate them from *Porcellidium* and *Acutiramus*. *Acutiramus* is maintained because it is clearly excluded by the new definition of *Porcellidium* in shape of the female genital double-somite, caudal rami, P5 and details of the male antennule. It is excluded from *Ravania* by the presence of T3 on the caudal ramus and structure of the male antennule.

The case for placing *Clunia cocosensis* and *Geddesia quadrata* in separate genera is not so clear for they both have a pentagonal caudal ramus similar in shape to *Mucrorostrum yoroium*, but not found elsewhere in the family. However, the three species cannot be placed together in the same genus because of fundamental differences in the setation of their maxillule. This appendage shows remarkable uniformity in the number of setae on endites and the endopod throughout the Porcellidiidae and any deviation must be considered an autapomorphic feature. *Geddesia* has six setae on the endopod, the typical porellidiid condition, but *Mucrorostrum* has only two setae on the endopod and an endite formula 1-2-1. *Clunia* on the other hand, has only one endopod seta and an endite formula 2-3-1. These two unique differences in maxillule setation are considered autapomorphic characters defining *Mucrorostrum* and *Clunia*.

An unexpected consequence of re-describing the type species for *Porcellidium* is that about half of the species described in the literature do not belong to that genus. Either they do not share all the characters of the genus or they possess apomorphic character states that eliminate them from *Porcellidium* and place them in other genera. Of the 59 species listed in the literature, eight are inadequately described and cannot be placed in any known genus: *P. fulvum* and *P. interruptum* Thomson (1882), *P. tuberculatum* Wolfenden (1905), *P. affine* and *P. charcoti* Quidor (1906), *P. wolfendeni* Brady (1910), *P. scotti* Pesta (1935) and *P. malleatum* Vervoort (1964). However, they may prove valid species when accurately redescribed. Another seven are synonyms for other species: *P. dentatum* Claus (1860), *P. ovatum* Haller (1879), *P. lecanoides* Claus (1889), *P. sarsi* Bocquet (1948), *P. penicilliferum,* Tiemann (1978), *P. acutum* and *P. aoifuchidorum* Harris & Iwasaki (1996, 1997) and another three are juvenile stages: *P. subrotundum* Norman (1868), *P. rotundum,* and *P. australe* Brady (1910). This leaves 41 recognized species, but only 20 of these fit the diagnosis for *Porcellidium*. The remainder must be transferred to other genera.

Table 2 gives a check list of the 71 species belonging to the Porcellidiidae recognized in the present study. It reveals the genus to which species rejected from *Porcellidium* have been moved, together with the original author, geographical distribution and the size of holotype and allotype specimens.

Distribution of Australian Porcellidiidae

A list of 32 described species and their recorded presence on the east coast of Australia is given in Fig. 14, but sampling has not been uniform along the whole coast. Knowledge of the NSW porcellidiid fauna is based on extensive collection at 17 stations over a period of two decades, whereas data on the Great Barrier Reef rests on a single sample washed from a mixture of seagrass (*Zostera capricornia* ?) and *Halimedia* sp. at Green Island, Cairns.

Despite this, there appears to be a clear distinction between the species that occur in northern Queensland and those that are found south of the Tropic of Capricorn. Of the 27 species known from NSW, only four have been recorded from Hervey Bay, southern Queensland and only two of these have been collected as far south as Eden (*Acutiramus rufolineatus* and *A. quinquelineatus*). Two species, *Clavigofera pacifica* and *Synurus ctenocheirus*, are known from Japan, but none of the other species has been recorded beyond Australian shores. No New Zealand species has been found in Australian waters. Eight species are only known from single localities.

Table 1. A summary of characters used to define genera in the Porcellidiidae (§ autapomorphic character, † apomorphic character). * For types of coupling denticle arrangement see Harris (2014b, p. 162). Characters i to xxxiii are considered plesiomorphic. Alternative (apomorphic) characters, indicated within parentheses ( ), refer to other genera, see genera numbered 2–16 in this table.

1 ***Porcellidium*** **Claus, 1860** (type species *P. viride*) [20 species]
- i Spermatophore elongate. (11).
- ii Normally deposited ventrally on the female's genital double-somite. (11).
- iii Spermatophore ephemeral, shed before egg laying starts. (11).
- iv Female receives only one spermatophore during her life span. (11).
- v Female cephalosome semicircular, not truncated anteriorly. (5, 12, 15).
- vi Male cephalosome truncated anteriorly. (9, 13).
- vii Hyaline border to cephalosome. (3).
- viii Ducts of marginal glands open dorsal to hyaline border. (3).
- ix No honeycomb-like pattern of cuticular folds on cephalosome. (5, 10, 14). Dorsal organs absent. (14).
- x Male genital somite not fused to P5 baseoendopod and segment 4 of metasome. (12).
- xi Female genital double-somite posterior lobe broad, rounded. (2, 6, 7, 8, 12, 13, 14, 15).
- xii No striations (rugosity) on anterior lobe of female genital double-somite. (6).
- xiii Anterior and posterior lobes clearly indicated by notch or cleft. (7, 8, 12, 13, 15).
- xiv 50% or more of caudal furca enclosed in posterior arch of genital double-somite.
- xv Female caudal ramus rectangular, but T1 and γ setae may be recessed at external corner. (2, 7, 8, 9, 11, 12, 13, 15, 16).
- xvi Terminal setae T1 to T4 always present on caudal ramus.(8, 9, 11, 12, 13, 15, 16). Setae never pinnate clavate, Fig. 12R. (6).
- xvii T2 and T3 very close together, never lie parallel to posterior border. (2).
- xviii α and β setae on caudal ramus never very close together (i.e., not less than width of ramus). (10).
- xix No ridge plates on labrum. (10).
- xx No denticle or comb on segment 3 of male antennule; ventral process (blade or knob) may be present. (4, 7, 8, 9, 13).
- xxi Anterior process on segment 3 of male antennule with δ and δ' setae that point forward, not laterally. (4, 10).
- xxii Segment 4 of male antennule has three coupling denticles (shape variable, but never a brush-pad). (2, 3, 4, 6, 8, 9, 12, 13, 14, 15).
- xxiii Endites on maxillule with three or four setae each. (5, 9, 16).
- xxiv Endopod of maxillule with six setae. (5, 9, 16).
- xxv Coxae of maxillipeds touch in mid-line. (10, 14).
- xxvi Fimbriate process always present on basis of maxilliped. (10, 14).
- xxvii Exopod segment 3 of P2, P3 and P4 with three external setae. (12).
- xxviii Terminal pair of setae on segment 3 of female P3 and P4 endopod plumose. (10).
- xxix Female P5 shorter than genital double-somite. (2, 5, 6, 7, 8, 9, 11, 13, 14, 15).
- xxx No ventral expansion of falciform ridge on female P5. (7).
- xxxi Male P5 trapezoid with six setae (one lateral, five terminal). (12).
- xxxii Animals dorsoventrally flattened, oval or elliptical in outline.
- xxxiii No notch at distal end of falciform ridge on female P5. (7, 8, 12).

2 ***Acutiramus*** **Harris & Robertson, 1994** [12 species]
- i Female P5s reach beyond genital double-somite and caudal rami to touch one another posteriorly.
- ii Female caudal ramus rhomboid (not rectangular).
- iii Setae T1, T2 and T3 always present on male and female caudal ramus.
- iv T2 and T3 very close, may lie parallel to posterior border.

3 ***Tectacingulum*** **Harris, 1994** [2 species]
- i Hyaline membrane on ventral side of cephalosome.§
- ii Marginal glands open on ventral side of cephalosome.§
- iii Large area of short peg-like setules on segment 1 of P1 exopod.§
- iv False (cuticular) border to cephalosome.§

4 ***Murramia*** **Harris, 1994** [2 species]
- i Male antennule segment 3 δ' absent from anterior process.§
- ii Unique arrangement of denticles on male antennule (type E*).§

5 ***Brevifrons*** **Harris, 1994** [1 species]
- i Unique arrangement of denticles and setae on male antennule (unipinnate seta associated with sensory lobe on segment 4).§
- ii Maxillule formula for endite setae 2-2-1.§
- iii Maxillule with two setae on endopod.†
- iv Low honeycomb-like ridges on dorsal surface of cephalosome.†
- v Male and female cephalosome truncated anteriorly.†

6 ***Clavigofera*** **Harris & Iwasaki, 1996b** [5 species]
- i Anterior lobe of female genital double-somite with lateral band of ridged cuticle (rugosity).§
- ii Terminal setae T1 to T4 large, pinnately clavate.§
- iii Seta T1 identical in size to T2, T1 to T4 evenly spaced across posterior border of caudal ramus.§
- iv Setae T1 and γ not recessed at lateral corner.†

Continued on next page

Table 1—*Continued*

7 *Kushia* Harris & Iwasaki, 1996b [4 species]
- i Female P5 with ventral expansion to falciform ridge.§
- ii Male antennule segment 3 with anterior comb-like denticle.§
- iii Unique arrangement of denticles on male antennule segment 4 (type C*).§

8 *Kensakia* Harris & Iwasaki, 1997 [5 species]
- i Brush-pad on segment 4 of male antennule.§
- ii Unique arrangement of denticles on male antennule (type A*).§
- iii Seta T2 absent from female caudal ramus.§
- iv Female caudal ramus trapezoid.†
- v T3 absent from male and female caudal ramus.†

9 *Mucrorostrum* Harris & Iwasaki, 1997 [1 species]
- i Unique arrangement of denticles on male antennule, four identical denticles on segment 4 (type D*).§
- ii Maxillule formula for endite setae 1-2-1.§
- iii Maxillule with two setae on endopod.†
- iv Female caudal ramus pentagonal, medial corner 90°.†
- v Animals can conglobate.†

10 *Dilatatiocauda* Harris, 2002 [7 species]
- i Labrum with two grooved plates (ridge plates).§
- ii Terminal pair of setae on female P3 and P4 endopod long, straight spinous setae (usually serrate).§
- iii Fimbriate process absent from maxilliped basis.§
- iv Coxae of maxilliped wide apart.†
- v Segment 5 of male antennule with lateral lobe.†
- vi Large areas of short peg-like setules on segment 1 of P1 endopod.†

11 *Porcelloides* Harris, 2014a [2 species]
- i Spermatophore reniform with recurrent duct.§
- ii Spermatophore deposited on dorsal surface of female P5, firmly attached by adhesive.§
- iii Spermatophore semipermanent on female, remains attached long after egg laying starts.§
- iv Deposition of more than one spermatophore on female common (1–4 may be present, implying that more than one male has deposited them).§
- v Unique arrangement of denticles on segments 4 of male antennule (type G).§
- vi Outline of male and female body ovate (egg-shaped), very little dorsoventral flattening.†
- vii Animals can conglobate.†

12 *Synurus* Harris, 2014b [2 species]
- i Male genital somite fused to metasome segment 4 and P5 baseoendopod.§
- ii Epipleural lobe of male metasome segment 4 very long (stretches back to extremity of caudal furca).§
- iii Male P5 ovate.§
- iv Male P5 with lateral seta, terminal setae atrophied or absent.§
- v Seta T1 absent from male and female caudal ramus.§
- vi Segment 3 of P2, P3 and P4 exopod with only two external setae.§
- vii Male cephalosome deeply concave anteriorly.†
- viii Anterior of female cephalosome truncated.†

13 *Ravania* gen. nov. Harris, 2014b [3 species]
- i Unique arrangement of denticles on male antennule (type B*).§
- ii Seta T3 absent from caudal ramus.†
- iii Male cephalosome semicircular anteriorly, not truncated.†

14 *Cereudorsum* gen. nov. [1 species]
- i Unique structure of male antennule (segment 4 with swollen finger-like structures in place of normal coupling denticles).§
- ii Dorsal organs.§
- iii Massive honeycomb-like cuticle surrounds dorsal organs.§
- iv Marginal glands open through numerous microtubules at edge of cephalosome (female only) §?
- v Reduction or absence of fimbriate process on basis of maxilliped.†
- vi Coxal lobes of maxillipeds wide apart.†

15 *Geddesia* gen. nov. [2 species]
- i Unique arrangement of male antennule (bulbous structures and denticles on segment 4) §?
- ii Anterior of female cephalosome truncated.†
- iii Male cephalosome deeply concave anteriorly.†
- iv Female caudal ramus pentagonal, medial corner 90°.†
- v T3 absent from male and female caudal ramus.†

16 *Clunia* gen. nov. [1 species, no male available]
- i Maxillule endopod with only one seta.§
- ii Maxillule formula for endite setae 2-3-1.§
- iii Female caudal ramus pentagonal, medial corner 90°.†
- iv T3 absent from caudal ramus.†

Key to the genera of Porcellidiidae

The following key to the above genera is based on features that can usually be seen on whole animals in dorsal and ventral view except for the denticles on the male antennule which require the antennule to be fully extended. The shape and setation of the female caudal ramus are easily seen and can be used to identify species and genera. The range in shape and setation of the female caudal ramus is extensive, but not easy to define in words. Figure 12 shows diagrammatically the basic shapes referred to in the key.

Multiple characters are given for each genus in the key, but confirmation of identity should be made by reference to Table 1 and the original descriptions of genera.

1 Body egg-shape (ovoid). Females carrying eggs may have one or more spermatophores attached to P5s. Female caudal ramus trapezoid (Fig. 12A, B), T2 always present, T3 may be present or absent. Male antennule[b] segment 4 with large denticulate pad (never brush-pad) ..... *Porcelloides*

—— Body outline oval or elliptical. Females carrying eggs never have spermatophore attached (lost before egg laying starts). Female caudal ramus trapezoid, T2 and T3 always absent (Fig. 12C). Male antennule[b] segment 4 with brush-pad. (Fig. 12Q) ..... *Kensakia*

—— Body outline oval or elliptical. Females carrying eggs never have spermatophore attached (lost before egg laying starts). Female caudal ramus rectangular, pentagonal or rhomboid. Male antennule segment 4 denticles variable in shape and number but never a brush-pad 2

2 Hyaline membrane with sensilla on ventral surface of cephalosome, false cuticular border to cephalosome. Ducts of marginal glands open on ventral surface of cephalosome ..... *Tectacingulum*

—— Hyaline membrane with sensilla forms lateral border of cephalosome. Ducts of marginal glands open on dorsal surface of cephalosome 3

3 Coxal lobes of maxillipeds wide apart 4

—— Coxal lobes of maxillipeds touch in midline 5

4 T1 and γ not deeply recessed at lateral corner of female caudal ramus, setae T1–T4 slender, T2 and T3 very close together. Terminal pair of setae on P3 and P4 endopod long, straight spinous (not plumose). No massive dorsal cuticular honeycomb ..... *Dilatatiocauda*

—— T1 and γ setae deeply recessed at lateral corner of female caudal ramus, T1 slender, T2, T3 and T4 large, pinnate, equally spaced. Massive cuticular honey-comb on back ..... *Cereudorsum*

5 Female caudal ramus rectangular, setae T1 and γ not recessed, T1, T2, T3 and T4 large, pinnately clavate (Fig. 12D, R), equally spaced across posterior edge. Lateral ridges (rugosities) on anterior lobe of female genital double-somite ..... *Clavigofera*

—— Setae T1–T4 on female caudal ramus never pinnately clavate or equally spaced across posterior edge. No rugosities on female genital double-somite. Caudal rami may be rectangular, pentagonal or rhomboid 6

6 Female caudal ramus rectangular, may widen posteriorly, T1 and γ setae may *or* may not be recessed at lateral corner, T2, T3 and T4 attached to posterior edge, (Fig. 12E, F, G, H) 7

—— Female caudal ramus pentagonal, medial corner 90°, lateral corner with T1 and γ on sloping (bevelled) edge, T2 and T4 on straight posterior edge. (Fig. 12I), T3 absent 9

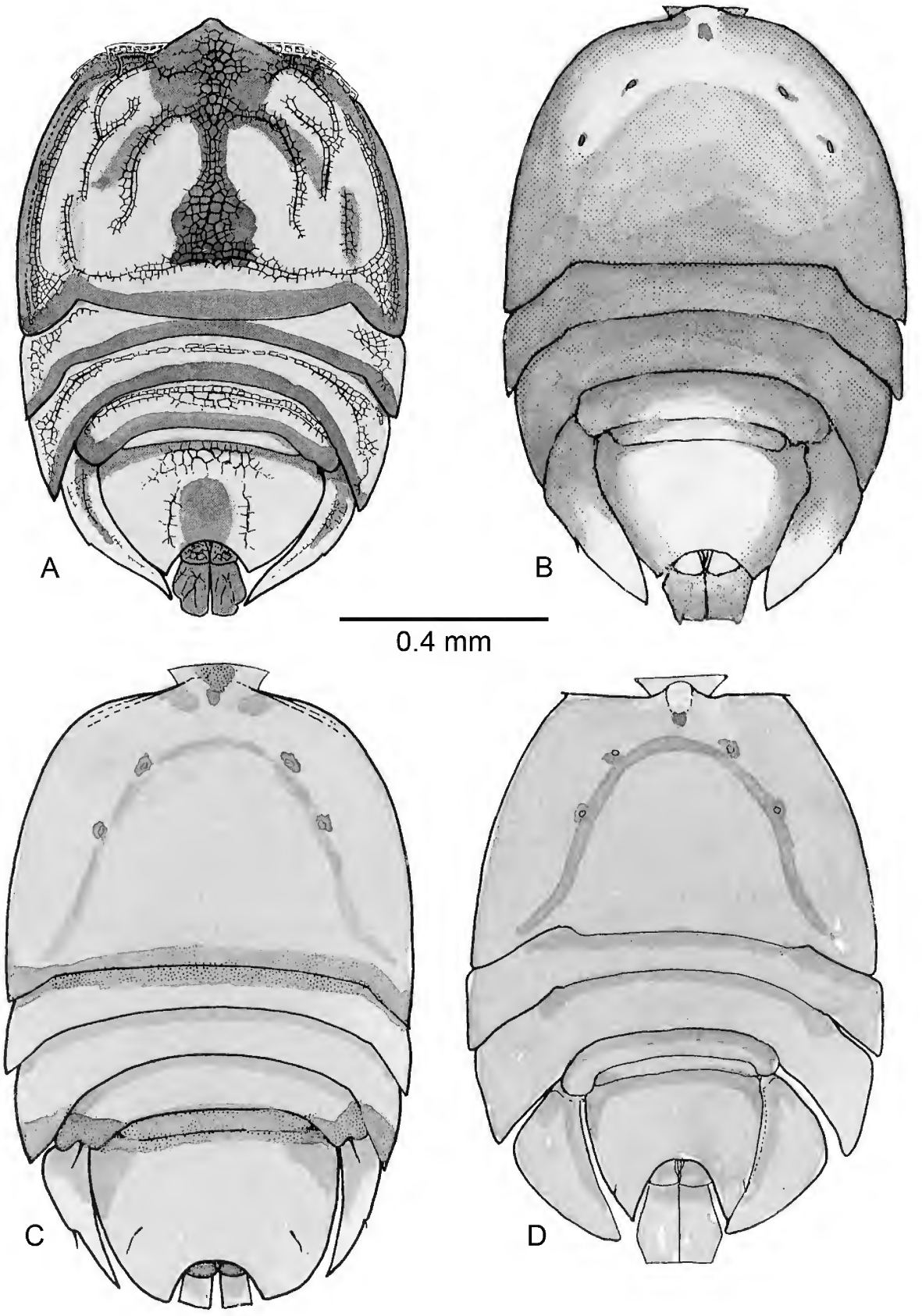

Plate 3. *(A) Brevifrons faviolatum* Harris, 1994, female. *(B) Mucrorostrum yoroium* Harris & Iwasaki, 1997, female, Japan. *(C) Murramia bicincta* Harris, 1994, female. *(D) Geddesia quadrata* sp. nov., female. All Australian species.

—— Female caudal ramus rhomboid or rounded posteriorly; terminal seta T2 always present, T1 or T3 may be absent (Fig. 12J or K, L); posterior edge straight at acute angle with medial edge (bevelled) and T4 at apex (Fig. 12M, N) *or* posterior edge convex with T4 at apex (Fig. 12K) *or* posterior edge may be rounded, no apex (Fig. 12 O) 10

7 Female caudal ramus lateral corner deeply recessed or bevelled bearing T1 and γ. T2 and T3 very close, T4 near medial corner, (Fig. 12G). Anterior comb on segment 3 of male antennule[b]. Falciform ridge of female P5 extended as ventral expansion (Fig. 12P). Maxillule[a] endopod with six setae ..... *Kushia*

—— Female caudal ramus with T1 and γ deeply recessed at lateral corner. T2, T3 and T4 evenly spaced across posterior border (Fig. 12H). Female genital double-somite narrow, pointed posteriorly. No comb on segment 3 of male antennule. No ventral expansion on female P5. Maxillule[a] with two setae on endopod. (Plate 3A, p. 190) ..... *Brevifrons*

—— Female caudal ramus may *or* may not be recessed (Fig. 12E, F).T2 and T3 very close, T4 near medial corner. Female genital double-somite broad, rounded posteriorly. No comb on segment 3 of male antennule. No ventral expansion on female P5. Maxillule[a] with six setae on endopod 8

8 Male antennule[b] δ' seta absent from anterior lobe, δ seta and one coupling denticle present on segment 3, ventral lobe (blade or knob) absent, segment 4 with four denticles (large denticulate pad plus three serrated denticles). (Plate 3C, p. 190) ..... *Murramia*

—— Male antennule[b] setae δ and δ' always present on anterior lobe of segment 3 but no coupling denticle, a ventral lobe (blade or knob) may be present, segment 4 with three denticles (shapes variable but never a brush-pad) ..... *Porcellidium*

9 Maxillule[a] endopod with six setae. Anterior of male cephalosome concave. Male antennule[b] segment 3 without a coupling denticle, segment 4 with two denticles. (Plate 3D, p. 190) ..... *Geddesia*

—— Maxillule[a] endopod with two setae. Anterior of male cephalosome semicircular (not truncated). Male antennule[b] with one denticle on segment 3, segment 4 with four denticles. (Plate 3B) ..... *Mucrorostrum*

—— Maxillule[a] endopod with one seta. (Male characters not known) ..... *Clunia*

10 Male P5 oval with one lateral seta, terminal setae absent or reduced to very small spines. Anterior of male cephalosome deeply concave. Seta T1 absent from caudal ramus, T3 present, (Fig. 12J). Female genital double-somite not divided into anterior and posterior lobes ..... *Synurus*

—— Male P5 trapezoid with six terminal setae. Anterior of male cephalosome semicircular. Seta T1 present, T3 absent from caudal ramus, (Fig. 12K, L). Female genital double-somite not divided into anterior and posterior lobes ..... *Ravania*

—— Male P5 trapezoid with six terminal setae. Anterior of male cephalosome truncated. Seta T1 and T3 present on caudal ramus, (Fig. 12M–O). Female genital double-somite divided into anterior and posterior lobes by notch, cleft or indentation ..... *Acutiramus*

[a] Study of maxillule setation requires dissection, but a maxillule with six setae on the endopod can usually be identified without dissection (see Fig. 13 for position of maxillule).

[b] The male antennule must be viewed from ventral aspect fully extended (see *Methods and terminology*). For different "types" of coupling denticle arrangement, see Harris (2014b, pp.161–162).

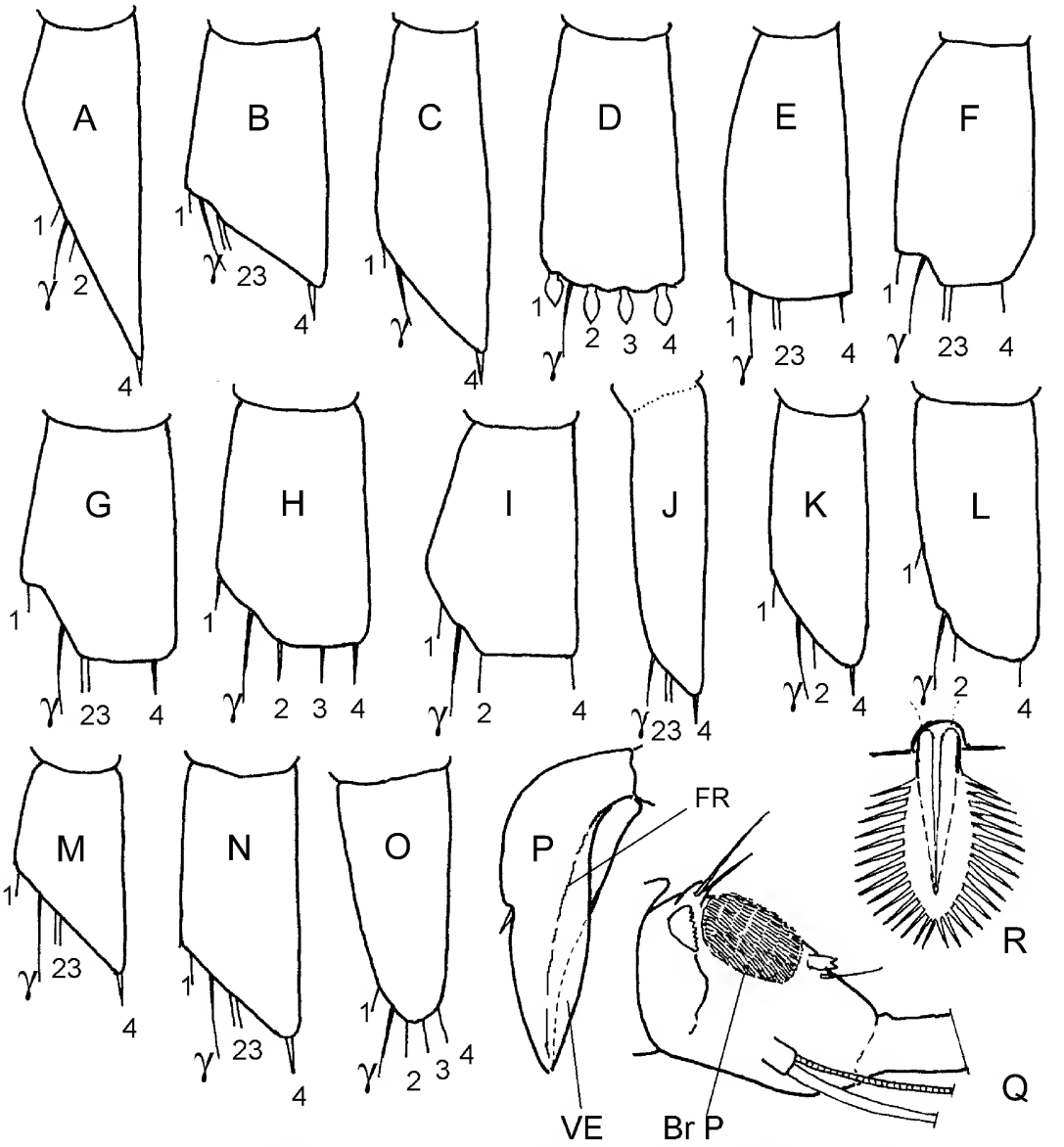

Figure 12. Types of female left caudal ramus and terminal setae found in the Porcellidiidae (α and β seta not shown). *(A, B) Porcelloides. (C) Kensakia. (D) Clavigofera. (E, F) Porcellidium, Tectacingulum, Murramia* and *Dilatatiocauda. (G) Kushia. (H) Brevifrons* and *Cereudorsum. (I) Mucrorostrum, Geddesia* and *Clunia. (J) Synurus. (K, L) Ravania. (M, N, O) Acutiramus. (P) Kushia,* female right P5 ventral view (*VE*, ventral expansion; *FR*, falciform ridge). *(Q) Kensakia,* male antennule (ventral view; *Br P,* Brush-pad). *(R) Clavigofera,* pinnate clavate terminal seta from caudal ramus.

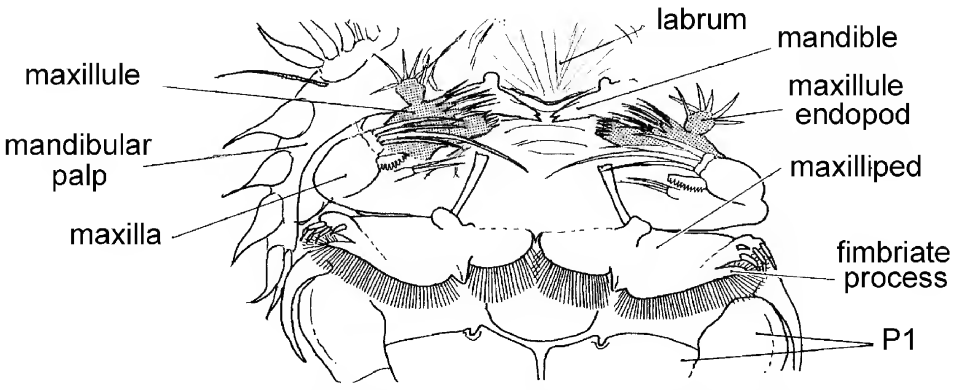

Figure 13. Ventral view of mouth region showing position of maxillule endopod, (*Mx1*, maxillule; *END*, maxillule endopod; *Mx2*, maxilla; *MXP*, maxilliped; *MDP*, mandibular palp; *MP*, molar process; *LAB*, labrum).

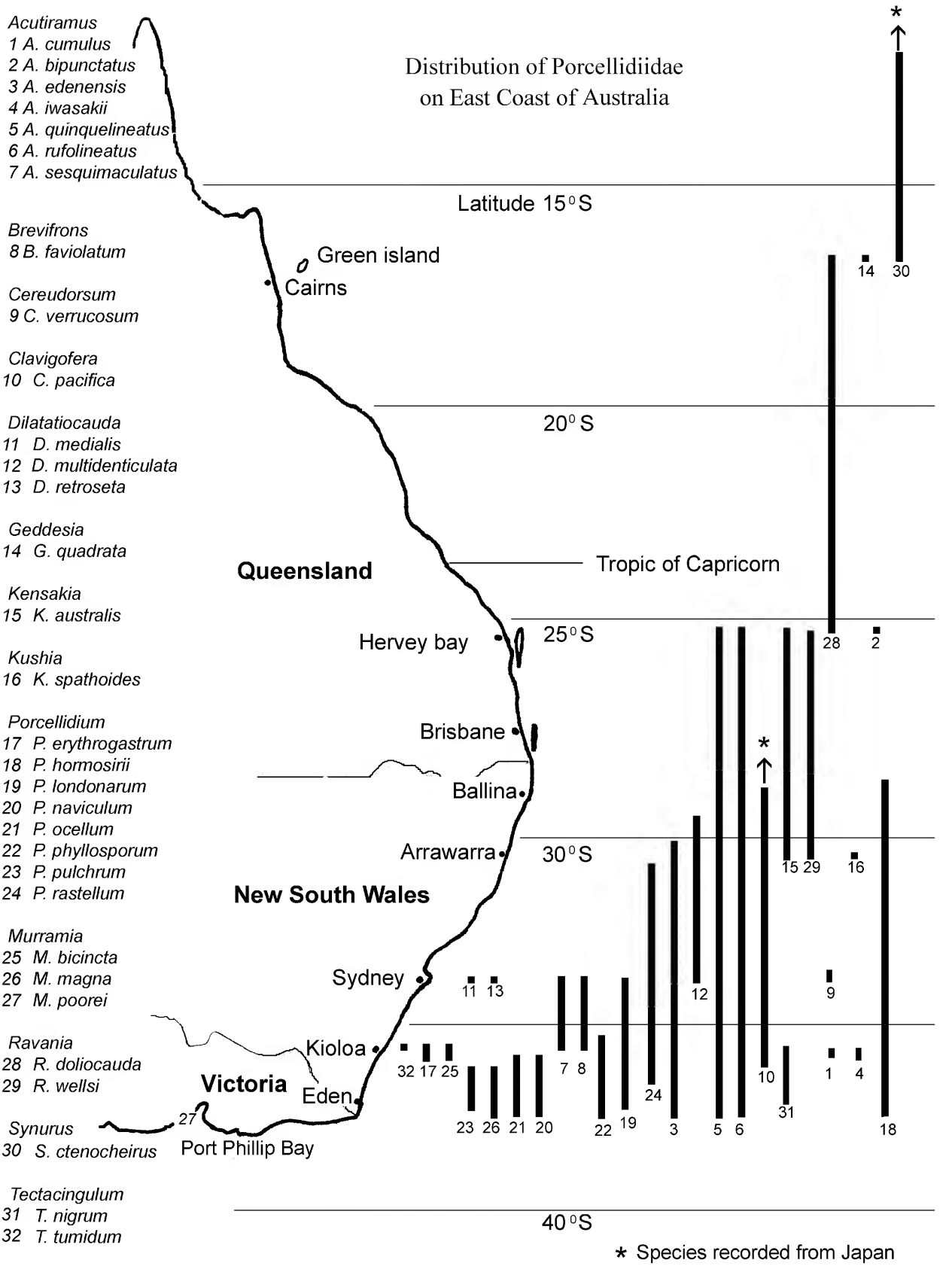

Figure 14. Australian Porcellidiidae. List of species and their known distribution.

Table 2. List of species sufficiently well described to be placed in a genus (in alphabetical order).

genus/species		original name and author	locality	size in mm female	male
PORCELLIDIDAE					
Acutiramus Harris & Robertson, 1994					
A. bipunctatus	1	Harris, 2014b	Qld[a] Australia	0.63	0.56
A. brevicaudatus	2	*Porcellidium brevicaudatum* Thompson & Scott, 1903	Sri Lanka/Madagascar/ Korea	0.78	0.53
A. cumulus	3	Harris, 2014b	NSW[a] Australia	0.78	0.55
A. edenensis	4	Harris, 2014b	NSW[a] Australia	0.67	0.49
A. geddesi	5	*P. ovatum* Geddes, 1968	W. Indies	0.62	0.51
A. iwasakii	6	Harris, 2014b	NSW[a] Australia	0.70	0.54
A. paguri	7	*P. paguri* Ho, 1986	Japan	0.56	0.46
A. quinquelineatus	8	Harris & Robertson, 1994	NSW/Qld Australia	0.55	0.43
A. rufolineatus	9	Harris & Robertson, 1994	NSW/Qld Australia	0.52	0.48
A. sesquimaculatus[b]	10	*Kioloaria sesquimaculata* Harris, 1994	NSW Australia	0.76	0.59
A. similis	11	*P. similis* Kim & Kim, 1996	Korea	0.76	0.50
A. tapui	12	*P. tapui* Hicks & Webber, 1983	New Zealand	0.69	0.51
Brevifrons Harris, 1994					
B. faviolatum	13	Harris, 1994	NSW Australia	1.00	0.83
Cereudorsum gen. nov.					
Cer.verrucosum	14	sp. nov.	NSW Australia	0.92	0.72
Clavigofera Harris & Iwasaki, 1996b					
Cla. clavigofera	15	*P. clavigerum* Pesta, 1935	Honolulu	0.5	?
Cla. echinophila	16	*P. echinophilum* Humes & Gelerman, 1962	Madagascar	0.57	0.43
Cla. laurencia	17	*P. laurencium* Hicks, 1982	South Africa	0.80	0.53
Cla. pacifica	18	Harris & Iwasaki, 1996b	Japan/NSW Australia	0.58	0.42
Cla. ulva	19	*P. ulvum* Hicks, 1982	South Africa	0.80	0.53
Clunia gen. nov.					
Clu. cocosensis	20	sp. nov.	Cocos Keeling Islands	0.97	—
Dilatatiocauda Harris, 2002					
D. bipartita	21	*P. bipartitum* Kim & Kim, 1997	Korea/Japan	1.70	1.00
D. dilatata	22	*P. dilatatum* Hicks, 1971	New Zealand	0.92	0.63
D. medialis	23	Harris, 2002	NSW Australia	0.92	0.70
D. multidenticulata	24	Harris, 2002	NSW Australia	0.84	0.58
D. plana	25	*P. planum* Tiemann, 1977	Mozambique	1.07	0.79
D. retroseta	26	Harris, 2002	NSW Australia	0.93	0.67
D. tristanensis	27	*P. tristanense* Wiborg, 1964	SW Africa	0.89	0.77
Geddesia gen. nov.					
G. quadrata	28	sp. nov.	Qld Australia	1.06	0.86
G. trisetosa	29	*P. trisetosum* Geddes, 1968	Bahamas	0.78	0.63
Kensakia Harris & Iwasaki, 1997					
Ke. acuta	30	*P. acutum* Kim & Kim, 1997	Korea/Japan	0.90	0.74
Ke. acuticaudata[c]	31	*P. acuticaudatum* Thompson & Scott, 1903	Sri Lanka/Maldives	0.65	0.50
Ke. australis	32	Harris, 2014b	Qld Australia	0.61	0.55
Ke. parva	33	Harris & Iwasaki, 2009	Malaysia	0.54	0.45
Ke. shimodensis	34	Harris & Iwasaki, 2009	Japan	1.06	0.81
Kushia Harris & Iwasaki, 1996b					
Ku. gamoi	35	Harris & Iwasaki, 1996b	Japan/Korea	0.64	0.62
Ku. igaguria	36	Harris & Iwasaki, 1996b	Japan	0.78	0.66
Ku. spathoides	37	Harris, 2014b	NSW Australia	0.74	0.68
Ku. zosteraphila	38	Harris & Iwasaki, 1996b	Japan	0.93	0.76
Mucrorostrum Harris & Iwasaki, 1997					
Muc. yoroium	39	Harris & Iwasaki, 1997	Japan	1.08	0.86
Murramia Harris, 1994					
Mur. bicincta	40	Harris, 1994	NSW Australia	1.07	0.86
Mur. magna	41	Harris, 1994	NSW Australia	1.38	1.21
Mur. poorei[d]	42	*P. poorei* Walker-Smith, 2001	Victoria[a] Australia	0.81	0.62

Continued on next page

Table 2—*Continued*

genus/species		original name and author	locality	size in mm female	male
Porcellidium Claus, 1860					
P. akashimum	43	Harris & Iwasaki, 1996a	Japan	0.84	0.69
P. algoense	44	Hicks, 1982	South Africa	0.61	0.46
P. brevicavum	45	Kim & Kim, 1997	Korea/Japan	0.73	0.63
P. erythrum	46	Hicks, 1971	New Zealand	0.57	0.48
P. erythrogastrum	47	Harris & Robertson, 1994	NSW Australia	0.83	0.61
P. fimbriatum	48	Claus, 1863	Europe	0.76	0.56
P. hartmannorum	49	Tiemann, 1978	SW Africa	0.76	0.55
P. hormosirii	50	Harris & Robertson, 1994	NSW Australia	0.68	0.50
P. kiiroum	51	Harris & Iwasaki, 1996a	Japan	0.81	0.58
P. londonarum	52	*P. londonii* Harris, 1994	NSW Australia	0.75	0.57
P. naviculum	53	Harris & Robertson, 1994	NSW Australia	0.72	0.57
P. ocellum	54	Harris & Robertson, 1994	NSW Australia	0.67	0.56
P. ofunatense	55	Harris & Iwasaki, 1996a	Japan/Korea	0.94	0.68
P. phyllosporum	56	Harris & Robertson, 1994	NSW Australia	0.93	0.73
P. pulchrum	57	Harris & Robertson, 1994	NSW Australia	0.71	0.55
P. rastellum	58	Harris, 2014a	NSW Australia	0.77	0.54
P. roscoffensis	59	*P. lecanoides* var. *roscoffensis* Bocquet, 1948	Europe	0.85	0.70
P. rubrum	60	Pallares, 1966	Argentina	0.69	0.61
P. viride	61	Philippi, 1840	Europe	0.91	0.62
P. wandoensis	62	Kim & Kim, 1997	Korea/Japan	0.69	0.61
Porcelloides Harris, 2014a					
Poi. scutatus	63	*Porcellidium scutatum* Claus, 1889	Europe	0.84	0.78
Poi. tenuicaudus	64	*Porcellidium tenuicauda* Claus, 1860	Europe	1.40	0.78
Ravania Harris, 2014b					
R. doliocauda	65	Harris, 2014b	Qld Australia	0.75	0.66
R. ravanae	66	*P. ravanae* Thompson & Scott, 1903	Sri Lanka	0.64	0.55
R. wellsi	67	Harris, 2014b	Qld Australia	0.57	0.51
Synurus Harris, 2014b					
S. ctenocheirus	68	Harris, 2014b	Qld Australia/Japan	0.68	0.48
S. unicus	69	*P. unicus* Ummerkutty, 1970	Sri Lanka	0.75	0.63
Tectacingulum Harris, 1994					
T. nigrum	70	Harris, 1994	NSW Australia	0.95	0.68
T. tumidum	71	Harris, 1994	NSW Australia	1.14	0.76

[a] NSW = New South Wales, Qld = Queensland.

[b] Transferred to *Acutiramus*, see Walker-Smith (2001).

[c] Placed in *Acutiramus* by Harris & Robertson (1994). Specimens labelled *Porcellidium acuticaudatum* in the NHM collection (1928.4.2.43) from Lake Timsâh, Ismalia do not have T2 or T3 on the trapezoid caudal ramus—diagnostic characters for *Kensakia*.

[d] Walker-Smith confirms that the male antennule is characteristic of *Murramia* (personal communication).

· The following may be valid species, but are omitted from this list because their description does not allow them to be placed in a genus; they require redescription, (*fulvum* and *interruptum* Thomson, 1882, *tuberculatum* Wolfenden, 1905, *scotti* Pesta, 1935 and *malleatum* Vervoort, 1964).

· The species recorded from South Australia by Nicholls (1941) cannot be identified from his descriptions and are not considered here.

Many species occur in large populations on particular species of algae or sea grass, for example *Porcellidium hormosirii* is abundant on *Hormosira banksii*, the dominant mid-littoral alga on the NSW coast, but neither species are found at Hervey Bay. *P. phyllosporum* has only been found on *Phyllospora commosa* and *P. naviculum* on *Cystophora moniliformis*. *Tectacingulum nigrum* and *Murramia bicincta* are only found on other species of *Cystophora* common on the southern coast of NSW. From Sydney to the northern coast of NSW *Dilatatiocauda multidenticulata* is abundant on *Sargassum* which replace the *Cystophora* species. This shows that porcellidiid copepods tend to select particular seaweeds, consequently their distribution will be influenced by the distribution of algal species.

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